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THE PRODUCTION OF COPPER, ZINC AND MOLYBDENUM DEFICIENCIES IN CROP PLANTS GROWN IN SAND CULTURE WITH SPECIAL REFERENCE TO SOME EFFECTS OF WATER SUPPLY AND SEED RESERVES

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Sand culture methods of general application to the study of micronutrient deficiencies in crops on a large scale have been described recently [4]). Experience has shown that provision of sufficient water of suitable purity for the study of copper, zinc or molybdenum deficiencies may present technical difficulties in large scale experiments when reliance is placed on glass stills. The mineral reserves in large seeds [13]) [18]) [22]) [24]) may delay the onset of acute deficiency symptoms in some crops. The importance of these points is considered in this paper. A preliminary note on effects of seed reserves has already appeared [11]).

METHODS

Culture methods.

The general methods and details of purification procedures used in this work have been fully described elsewhere [4]) and are only outlined here.

Plants were grown from seed in 1 gallon pyrex glass containers provided with a central drainage outlet. The outlet was covered by

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glass wool and a watch glass to retain the sand but allowed free drainage. All glassware was cleaned with detergent, strong acid and steaming.

Sand was purified as described previously. In 1950 and 1951 two-day and three-day treatments with acid were used and compared; in 1952 two days with acid and 1 day with alkali were allowed for copper and zinc deficiencies. For molybdenum deficiency treatments the sand was treated for 3 days with acid and 1 day with alkali.

In 1950 water was obtained by distillation from pyrex glass stills of tap water already distilled from tinned copper stills with silver condensers. This once glass distilled water was compared with water purified by three other methods; water distilled twice from glass, water distilled from tinned copper stills with pyrex glass condensers and rain water purified by ion exchange resins. In 1952 once glass distilled water and purified rain water were compared. The resins used were Permutit Zeocarb 215 and Deacidite E resins followed by IMAC C11 cation resin in 1951 and by Permutit Biodeminrolit FF mixed-bed resin in 1952, contained in a pyrex glass column measuring 75 cm × 12.5 cm and holding about 15 l of resin. The rate of flow was 6–10 l/hour. The resin treated water was also used for the whole of the experimental work on seed reserves in 1952.

The nutrient solutions were prepared from suitably purified stock solutions [4]). The main constituents were provided at the following concentrations as me/l NO_3^- 15; PO_4^{---} 4; Ca^{++} 10; K^+ 5; Mg^{++} 3; Fe^{+++} 0.3. Micronutrients were given as stated previously, *loc. cit.*

Plant material.

The crops grown during the 3 years were — tomato (Market king), oat (Star), wheat (Atlee), maize (Golden bantam), red clover (Dorset marl), alsike clover, lucerne (Provence), runner bean (Scarlet emperor), dwarf bean (Masterpiece), broad bean (Longpod), pea (Onward), sugar beet (Webbs No. 2), swede (Purple top).

Commercial seed was used in all years for each crop. In addition, seed was saved in 1951 from peas, broad, runner and dwarf beans grown in sand cultures given complete nutrient solutions or solutions deficient in copper, zinc and molybdenum respectively and re-sown in cultures given these respective treatments in 1952 for comparison with fresh commercial seed of the varieties used.

Analytical methods.

Samples of foliage were collected at the end of each year's experiment, dried in a steam oven and redried before analysis. Seeds were sampled from the air-dried mature seeds saved for sowing again or stored from the previous year. Dried material was digested with nitric and perchloric acids and evaporated to dryness. The residue was dissolved in boiling water, filtered and made to a convenient volume. Copper and zinc were determined in the same aliquot by a method based on that of Piper [17]) using purified dithizone [16]) but modified to include the addition of thiosulphate to increase the specificity of the method for zinc [1]) [21]).

Molybdenum was determined in a separate aliquot of the acid digest solution by the method of Piper and Beckwith [19]) slightly modified for use with 8 ml 1 cm absorption cells and with omission of the dithizone extraction stage since no interference due to copper was found with our material.

Layout.

Treatments were replicated in randomised sub-blocks, in which the respective deficiency or complete nutrient treatments were segregated to avoid risks of contamination by splashing during the application of the solutions. In order to ensure as far as possible that comparisons between the use of commercial and "sand culture" seed were made under similar conditions plants were grown from both the commercial and the respective "deficiency" seeds in the *same* pots and were thus independent of any variations in nutrient supply or environment.

RESULTS

Effects of sand treatment.

Visual comparison and yield data in Table I showed there was no appreciable increase in the severity of copper and zinc deficiencies in 1951 when the sand was treated for 3 days with acid instead of 2 days. Results for zinc deficiency in 1952 (Table II) were outstandingly and consistently more severe than those obtained previously. This was tentatively attributed to the quality of the sand and possibly to the inclusion of the alkaline treatment which was already considered advantageous for production of molybdenum deficiency [4]). There was no effect on severity of copper deficiency.

TABLE I

Yields g dry weight per plant of crops grown in 1951 water supply test

Crop and source of water supply	Sand treatment	Copper deficiency		Zinc deficiency		Crop and source of water supply	Molybdenum deficiency	
		Dry wt. g	% of control	Dry wt. g	% of control		Dry wt. g	% of control
Tomato:						*Tomato:*		
Metal stills	2 days	14.9	24.2	21.7	35.7	1 × glass distilled	16.6	27.4
	3 ,,	13.4	22.2	24.2	38.8	Resin treated rain water. .	21.3	34.8
1 × glass distilled	2 days	2.3	3.8	14.8	24.2	*Red Clover:*		
	3 ,,	1.6	2·7	14.5	24.0	1 × glass distilled	4.0	34.9
2 × glass distilled	2 days	1.9	3.2	14.0	23.0	Resin treated rain water. .	3.1	25.2
	3 ,,	1.4	2.3	20.6*	33.8			
Resin treated rain water.	2 days	3.3	5.4	16.7	27.6	*Sugar beet:*		
	3 ,,	1.2	1.9	17.0	28.1	1 × glass distilled	4.0	7.2
Red clover:						Resin treated rain water. .	7.6	13.5
Metal stills	2 days	6.5	56.2	8.4	72.4	*Lettuce:*		
	3 ,,	8.0	69.7	8.8	75.6	1 × glass distilled	0.28	1.3
1 × glass distilled	2 days	0.21	1.7	4.3*	37.2	Resin treated rain water. .	0.15	0.7
	3 ,,	0.32	2.6	1.8	15.6	*Carrot:*		
2 × glass distilled	2 days	0.16	1.3	4.8*	41.5	1 × glass distilled	2.6	—
	3 ,,	0.20	1.7	7.5*	64.8	Resin treated rain water. .	1.3	—
Resin treated rain water	2 days	0.46	3.9	2.8	24.2	*Swede:*		
	3 ,,	0.68	5.9	3.1	26.4	1 × glass distilled	23.4	—
						Resin treated rain water. .	24.3	—
						Radish:		
						1 × glass distilled	21.5	—
						Resin treated rain water. .	25.3	—

*) Probably contaminated by condensation or paint from roof.

TABLE II

Yields g dry weight per plant; crops grown in 1952 water supply test							
Crop	Copper deficiency		Zinc deficiency		Molybdenum deficiency		Complete nutrient
	Glass distilled water	Resin treated rain water	Glass distilled water	Resin treated rain water	Glass distilled water	Resin treated rain water	Resin treated rain water
Tomato							
44 days	0.23	0.24	0.08	0.07	0.43	0.36	2.26
90 days	1.25	1.02	0.30	0.35	1.12	1.42	81.5
Red clover							
44 days			0.09	0.05	0.11	0.13	0.22
90 days			0.06	0.05	0.43	0.75	7.00
Wheat							
86 days	0.60	0.60					9.13

Effects of water supplies.

The yields of crops grown in the water supplies tests are shown in Tables I and II. The data were confirmed by visual observations of the crops in each test. It is evident that the provision of pyrex glass condensers is not an effective safeguard against serious heavy metal contamination in water obtained from tinned copper stills, and that the extent of the contamination is sufficient to interfere seriously with experiments on copper and zinc deficiencies. On the other hand, rainwater purified by ion-exchange resins may compare satisfactorily with glass distilled water and attains the exacting standards necessary for the production of severe deficiencies of copper, zinc and molybdenum whilst providing the copious supplies required for large scale methods. A single charge of resin provided over 15000 l of consistently satisfactory water in 5 months, at rates of flow up to 10 l/hour.

There was a slight advantage for glass distillation in 1951 compared with use of the IMAC C11 resin. The advantage disappeared or was reversed later in the season as regards molybdenum content, when judged either by changes recorded visually or by yields in the respective treatments. In 1952 results with water treated with the Biodeminrolit mixed bed resin were comparable to those of the glass distilled water for all three deficiencies. The Biodeminrolit was concluded to be more suitable for the present purpose than the IMAC C11 resin. Comparative effects are illustrated in Plate I.

Although not listed here, severe molybdenum deficiency was

produced in lettuce, cauliflower and Brussels sprouts grown throughout the test, with solutions made up in the Biodeminrolit treated rain water and effects were as severe as those previously recorded [9] [10].

TABLE III

Yields g dry weight per plant of crops grown in copper and zinc deficient sand cultures in 1950 and 1951 experiments.

Crop		Copper deficiency		Zinc deficiency	
		dry wt.	% of control	dry wt.	% of control
Tomato	1950	1.5	1.0	19.5	12.6
Swede	1950	4.9	4.5	5.1	4.7
Sugar beet	1950	7.1	6.8	32.1	31.0
Oat	1950	1.9	24.1	3.6	46.2
Alsike clover	1950	2.0	5.4	1.6	4.3
,, ,,	1951	0.19	1.6	5.0	42.0
Lucerne	1951	0.15	1.4	5.6	53.7

Visual symptoms.

Systematic notes on effects of copper and zinc deficiencies have already been given for many of the crops [7] [8]. Only the more important general effects and fresh observations are therefore presented here. Characteristic examples are shown in Plates III, IV and V.

Copper deficiency: The relation of leaf age to incidence of symptoms depended on the particular crop. Young leaves or the growing point were principally affected in wheat, oat, broad bean and lucerne. Profuse tillering or branching occurred in this group. Old leaves were more sensitive in dwarf bean, tomato, clovers and swede. Foliage was often dull olive green, or grey-green, but was abnormally dark blue-green in tomato and lucerne. Tomato plants grown with slightly more copper obtained from the water from metal stills showed pronounced yellow and purple tints of older leaves and the upcurling of leaf margins associated with severe deficiency was absent. Characteristic necrotic patterns along major veins developed in dwarf and runner bean leaflets. Effects of "white tip" disease in oats do not require description; wheat, however, showed in addition, a characteristic coiling of the chlorotic or pale rolled leaf tips, which was often reversed midway in a manner suggestive of the tendrils of certain climbing plants.

Most plants of the large seeded legumes produced a few seeds but peas, which produced normal sized pods, were entirely devoid of

seed. Flowering was prevented in the smaller seeded clovers, tomato and cereals.

Zinc deficiency: Many crops showed effects suggestive of acute phosphorus deficiency. This was especially so for maize, swede, clovers, pea and the beans. Foliage became dull olive green and faded. Purple or bronze tints were produced in maize, beans and clovers. "Little leaf" effects due to reduction in the breadth of the lamina appeared in the upper leaflets of broad bean and in leaflets of runner bean when severe deficiency was produced in 1952. Crinkling or wavy outlines of leaf margins developed in runner bean and in clovers which also became involute at the apex. The leaflets of runner bean and tomato showed marked asymmetry. They tended to become concave on the distal margin of the lateral leaflets of runner bean or of any leaflets of tomato. Runner bean also showed a characteristic spotting in the form of numerous small, rounded, dark green areas against a more general chlorotic background. Leaflets tended to remain folded in the clovers and in 1952 sudden breakdown and death of red clover seedlings was common. This was apparently associated with the growth of saprophytic fungi in the dying seedlings and was preceded by necrotic spotting of young leaves, and collapse of petioles. Leaflets of tomato plants curled downwards and sometimes completely round. Cell contents diffused out to the exterior of the leaves and collected in the hollows where saprophytic organisms were able to grow. A similar escape of cell contents which appeared as clear brown fluid that dried out as a white deposit occurred in maize and also in oats grown in 1953. Various types of necrosis were also common. These included effects resembling "grey speck" caused by lack of manganese in oat, breakdown in main and lateral petioles or major veins in tomato and necrosis of undersides of leaf veins in dwarf bean. As in copper deficiency the age of leaf affected was not consistent. Thus younger leaves were more sensitive in broad bean whereas older leaves were first involved in peas and tomato.

Molybdenum deficiency: Symptoms of severe molybdenum deficiency which developed in lettuce, tomato, red clover, cauliflower, Brussels sprouts and others grown as test crops to study the effects of water supplies have already been described [9] [10].

The following effects observed in the leguminous crops apply mainly to plants raised from impoverished seed. In pea and runner

bean they showed as a uniform grey-green or yellow chlorosis followed by sudden wilting and withering of the older leaves. Flowering was suppressed and plants died prematurely. Broad bean and dwarf bean were less sensitive but sudden wilting and drying out of large areas of leaflets occurred in dwarf bean and blackened scorching of older leaves occurred in broad bean; this was preceded by sunken intervenal areas which were wilted and grey-green in colour. Symptoms usually developed suddenly, often overnight, as recorded by M e a g h e r *et al.* [13]).

Effects of seed reserves.

Removal of cotyledons from dwarf and broad bean immediately after emergence of the shoot in 1951 resulted initially in reduced growth (Table IV). This effect persisted in broad bean in control plants but was not maintained in dwarf beans. Comparison of the growth of similarly excised plants in the deficiency treatments showed an additional response in each treatment but this was least

TABLE IV

Relation of seed origin to yields, g dry weight per plant, of large seeded leguminous crops grown in copper, zinc or molybdenum deficient sand cultures

Crop and seed origin		Treatment			
		Copper deficiency	Zinc deficiency	Molybdenum deficiency	Complete nutrient
Runner bean	1951 commercial source	19.0	19.5	77.3	97.5
	1952 commercial source	49.8	39.8	147.3	117.8
	1952 saved from 1951 sand culture	12.2	12.5	22.8	—
Dwarf bean	1951 entire seed commercial source	10.8	16.3	46.0	58.2
	1951 cotyledons excised	7.0	12.2	33.0	55.5
	1952 commercial source	31.0	11.1	118.3	73.1
	1952 saved from 1951 sand culture	1.1	4.6	32.3	31.9
Broad bean	1951 entire seed commercial source	12.1	7.6	50.7	54.1
	1951 cotyledons excised	1.5	5.5	34.7	40.1
	1952 commercial source	46.7	26.8	55.6	66.2
	1952 saved from 1951 sand cultures	2.9	12.5	25.6	50.0
Pea	1951 commercial source	7.3	4.3	24.4	19.9
	1952 commercial source	—	7.2	55.6	26.1
	1952 saved from 1951 sand culture	—	4.6	25.6	23.0

noticeable for molybdenum deficiency. The effect was most consistent for dwarf beans but the greatest depression was obtained with copper deficiency in broad beans. The visual effects of these excision tests were evident in dwarf bean after about 7 days in all treatments. No visual symptoms were produced in the molybdenum deficient plants, but copper and zinc deficiencies were accentuated.

The effects of using impoverished seed in 1952 were, however, far more striking than those of cotyledon excision (Table IV). The plants raised from seed grown in complete nutrient sand cultures the previous year were normal and not visibly distinguishable from those raised in the same pot from commercial seed in the control treatment with complete nutrient. Yields were, however, smaller and the effect varied with the crop. Plants raised from deficient seed were strikingly reduced in growth and showed far more severe symptoms in all respective deficiency treatments when compared with plants in the same pot, grown from commercial seed. The contrast was greatest for molybdenum deficiency where symptoms were only seen visually in such impoverished plants. Runner bean and pea were most sensitive visually whilst dwarf bean and broad bean did not respond until much later in the experiment. In terms of yields, however, peas were the least responsive (Table IV).

Copper deficient seeds were next in order of contrast but the reserves of commercially raised seed were not sufficient entirely to prevent the appearance of deficiency symptoms in 1952 as was found for molybdenum. Runner bean and broad bean seemed most sensitive to the difference. Zinc deficiency was least influenced by the status of seed reserves but the effect was still evident both in yield (Table IV) and in the time required for visual symptoms to develop. Runner bean and broad bean again appeared to be the most sensitive to the difference in origin of seed. Examples of the effects of seed reserves are shown in Plate II and Plate IIId

Analytical data.

Tables V and VI show the copper, zinc and molybdenum contents of seeds, and of foliage of plants derived from seed of different nutrient status. Tables of significance are given in Table VII. The concentrations of these elements and the total amount per seed shown in Table V varied considerably between different years for commercial seed or between commercial seed and that obtained

TABLE V

Relation of seed origin to copper, zinc and molybdenum content of the seed of large seeded leguminous crops

Crop	Seed origin *)	Copper		Zinc		Molybdenum	
		ppm	µg/seed	ppm	µg/seed	ppm	µg/seed
Runner bean	C 1951	5.11	3.53	8.17	5.69	0.52	0.36
	C 1952	2.29	2.39	16.9	17.7	0.19	0.20
	S complete nutrient	4.75	2.93	29.2	18.0	2.33	1.44
	S deficiency treatments	less than 0.051	less than 0.013	11.5	3.89	0.28	0.11
Broad bean	C 1951	8.59	8.48	14.2	14.1	1.14	1.13
	C 1952	8.10	16.8	22.5	46.8	3.64	7.54
	S deficiency treatments	—	—	—	—	0.13	0.14
Dwarf bean	C 1951	3.74	1.83	31.8	15.4	2.32	1.21
	C 1952	4.50	2.40	25.8	13.8	6.11	3.25
	S complete nutrient	8.31	3.99	41.7	20.1	5.95	2.87
	S deficiency treatments	less than 0.037	less than 0.010	8.15	3.87	0.11	0.04
Pea	C 1951	8.26	2.58	7.34	2.30	0.91	0.28
	C 1952	4.17	1.20	24.2	6.04	0.57	0.16
	S complete nutrient	2.89	0.80	16.9	4.68	3.02	0.83
	S deficiency treatments	—	—	11.5	3.72	0.24	0.07

*) C Commercial seed for the year shown.
S Seed saved from plants grown in respective sand cultures.

from plants grown in complete nutrient sand cultures. Still greater differences were found when seed raised from complete nutrient sand cultures was compared with that obtained from deficiency treatments. The nutrient status of such deficient seed was usually also drastically reduced when compared with seed of commercial origin. The relative decrease was greatest for copper in the instances where material was available for analysis and least for zinc. The molybdenum content of commercial broad bean and dwarf bean seed was apparently adequate for the normal growth of plants produced from them.

The analysis of foliage samples given in Table VI showed that the use of deficient seed saved from sand cultures did not have any great or consistent effect on the content of the deficient element in

TABLE VI

Relation of treatment and seed origin to copper, zinc and molybdenum content of foliage of large seeded leguminous crops grown in sand cultures

Treatment		Copper deficiency	Zinc deficiency	Molyb-denum deficiency	Complete nutrient		
Crop	Seed origin *)	ppm Cu	ppm Zn	ppm Mo	ppm Cu	Zn	Mo
Runner bean	C 1951	4.1	22.6	0.045	8.0	28.9	1.4
	C 1952	2.3	27.5	0.025	5.7	25.0	1.2
	S	3.1	25.4	0.030	—	—	—
Broad bean	C 1951	5.5	15.3	0.41	8.7	41.2	2.3
	C 1951 cotyledons excised	0.4	6.2	0.27	3.5	32.0	2.4
	C 1952	2.6	9.4	0.029	9.1	30.7	—
	S	3.9	3.8	0.085	9.0	18.4	0.85
Dwarf bean	C 1951	3.3	22.5	0.067	4.8	43.3	1.5
	C 1952	1.9	13.0	0.11	6.8	16.3	0.50
	S	6.0	8.9	0.058	12.1	17.0	0.76
Pea	C 1951	6.7	15.5	0.060	11.6	46.0	2.0
	C 1952	—	12.9	below 0.01	7.8	11.7	0.48
	S	—	21.7	below 0.01	23.0	26.5	0.39

*) C Commercial seed for year shown.
S Seed saved from plants grown in respective sand cultures.
Plants produced from C 1952 and S seed were grown adjacent in the same containers in each respective treatment.

the leaves when compared with material obtained from commercial seed and no differences were significant. The effect of using deficient seed was shown in the yield data and was therefore reflected mainly in *total content* of the element rather than in its concentration in the plants. On the other hand, deficiency treatments usually resulted in reduced concentrations of the respective elements compared with effects of the complete nutrient treatment irrespective of the origin of the seed, or the fact that plants were grown from the two sources of seed in the same container. There were occasional varietal differences summarised in the tables of significance (Table VI).

The relative decrease in concentration due to deficiency conditions was generally least for zinc and greatest for molybdenum although the latter was present in the least amount. Thus, the effect of deficiency treatments on nutrient content of foliage differed from that on the accumulation of nutrients in seed, as regards the *relative* effects for the different elements.

TABLE VII

Tables of significance of treatment effects for analytical data on copper, zinc and molybdenum in leaves and seeds of large seeded leguminous crops grown in sand culture

1951 Harvest: leaves from commercial seed

Effect of Cu deficiency on content		5%
,, Zn ,, ,,		5%
,, Mo ,, ,,		1%
,, varieties × treatments		1%
,, varieties (Mo) on content		0.1%
,, varieties (Cu) ,,		5%

Variety × treatment interactions were tentatively ascribed to the higher molybdenum content of broad beans and the higher copper content of pea and broad beans.

1952 Harvest: leaves from commercial or "sand culture" seed

Effect of Cu deficiency on content	1%
,, Zn ,, ,,	n.s. block replicate values varied widely
,, Mo ,, ,,	5%
,, seed origin ,,	n.s.
Origin of seeds × varieties	n.s.
,, seeds × treatments	n.s.
Varieties × treatments	n.s.

1951/52 Seeds obtained commercially or saved from sand culture plants; for data in terms of μg metal per seed

	(*i*)		(*ii*)	
Effect on Cu:	Commercial seed *v.* control saved seed:	n.s.	Control *v.* deficiency saved seed:	—
,, ,, Zn:	Commercial seed *v.* control saved seed:	n.s.	Control *v.* deficiency saved: seed	F = 4.77 n = 2
,, ,, Mo:	Commercial seed *v.* control saved seed:	n.s.	Control *v.* deficiency saved seed:	F = 7.05 n = 2
,, of season: 1951/52		n.s.	Not significant at 5% owing to limited number of degrees of freedom	

Effect of varieties: Commercial seed:	5%;	attributed to the high concentration in broad bean and the low concentration in pea seeds.
,, ,, varieties: Saved seed:	1%;	attributed to low content of pea seed.
Interaction metals × varieties	1%;	ascribed to high Mo content in dwarf bean and generally low content in pea seeds.

Differences between Cu, Zn and Mo concentrations significant at 0.1% in each set; Zn > Cu > Mo.

The concentrations of the respective element found in the dried foliage of plants and the levels present in the complete nutrient solution permit an approximate estimate of the relative ratios of these values for each element as follows: Cu, 50–350; Zn, 180–700;

Mo, 8-45. The differences between the concentrations of copper, zinc and molybdenum in the foliage were significant at 0.1%. Corresponding ratios deduced for deficiency conditions when the respective treatments provided probably 0.001 ppm or less of Cu or Zn and 0.00001 ppm Mo in the nutrient solution in 1952 range as follows: Cu 2000-7000; Zn, 4000-27000; Mo, 1000-40000. The values for copper and zinc have maintained similar proportions but the ratio for molybdenum has notably increased to a similar level. The somewhat high ratios for zinc deficiency were not considered to be due to contamination of the cultures as identical treatments produced exceptionally severe effects in tomato and were also rapidly lethal for red clover, but all ratios would be inflated by the contribution from the seed.

DISCUSSION

The striking contrast between the effects of zinc deficiency seen in 1950 and 1951 and those recorded in 1952 suggests either that alkali-soluble zincates may occur in the sand or that successive batches differed markedly in available zinc content.

The water supply tests show beyond reasonable doubt that ion-exchange resins can be used to purify rain water to a degree comparable to distillation in all-glass apparatus. The former method provides a high output with little attention and should greatly assist in the maintenance of large scale culture experiments. The extent of molybdenum removal by the cation resin used in 1951 was less than that achieved in 1952. The average values found by *A. niger* [5]) assay were 0.000013 and 0.000008 ppm respectively as compared with an initial value of 0.0005 ppm. That the cation resin was so effective suggests either that reduction of molybdate occurred at the resin surface or that lower valency compounds of molybdenum were present in the rain water. The reduction of vanadium on ion-exchange resins has been shown recently [20]).

The results demonstrating the importance of seed reserves in determining the type of response to all three deficiencies and especially of molybdenum entirely confirm those of Meagher *et al.* [13]). Seed reserves will thus affect the uniformity of responses in experiments designed to study these deficiencies. The results also support the conclusion of Wilson [24]) on the origin and incidence of

"scald" in beans and explain our earlier failures [6] [10] to obtain marked effects from molybdenum deficiency in sand cultures with such large seeded species. Removal of the cotyledons was tested also in this earlier work without effect. Results in the present work suggest that this procedure is not very effective and the seed reserves are therefore presumably located in, or rapidly translocated to the plumule and radicle during the first 5–8 days of germination. Bertrand [2] recorded up to 50 ppm molybdenum in the embryos of bean seeds. A few instances were recorded (Table IV) in which differences between yields obtained from plants grown in successive years from commercial seed exceeded those found between plants grown from commercial or sand culture seed in 1952. Although comparisons between results obtained in different years are not strictly valid it is noteworthy that in the deficiency treatments these relative changes in yields often reflected the variations in the total content of the respective elements in the seed. Similar changes, though less in proportion, occurred with plants given the complete nutrient treatments. Yields obtained with molybdenum deficiency in 1952 were mainly greater than those recorded for plants given the complete nutrient treatment when grown from commercial seed and the molybdenum level in the complete nutrient may have exceeded at some stage the optimum concentration for these species already provided with apparently adequate reserves in the seed.

No explanation is possible at present for the slight reduction in growth of plants in the complete nutrient treatment as the result of using seed saved from previous cultures. The relative effects of the deficiency treatments were, however, much greater than this latter effect and left no doubt about the importance of seed reserves in the incidence of copper, zinc and molybdenum deficiencies in these large seeded species.

Leaf morphological effects produced by zinc deficiency in tomato, runner bean and broad bean were consistent with those already known to occur in other crops. The asymmetrical unilateral curvature in tomato and runner bean leaflets recalled the "sickle leaf" symptoms in cacao recently identified as zinc deficiency by Greenwood and Hayfron [3].

Millikan [14] [15] also observed the characteristic notching of subterranean clover leaflets deficient in zinc; leaflets of red or

al-like clovers grown in our experiments were not noticably thickened but no anatomical studies were made on microscopic structure. There is general agreement with Millikan [11]) and others, *loc. cit.* on the greater tolerance of lucerne to zinc deficiency, and confirmation of the great sensitivity of this species to copper deficiency and of the characteristic "die-back" of apical growth preceded by necrosis and dark blue-green foliage, but not of the epinastic effects noted by Millikan.

The exudation observed in zinc deficient tomato and maize, and also in oat (unpublished work) suggests that the cell membranes may have deteriorated with consequent loss of their capacity to retain cell solutes.

The analytical results show that the concentration of zinc may not always provide a reliable guide to a deficiency status and suggest that the level of 0.002 me l (0.065 ppm) given in the complete nutrient solution is still below the threshold for optimum growth of these crops. This view would be consistent with conclusions derived from a recent survey of literature on this point [4]) and with the results of Wilson [23]) who concluded that loblolly pine requires a minimum of 0.1 ppm Zn for normal growth. The lack of correspondence between depleted content in the seed of the three elements examined, and values found in foliage of deficient plants is also noteworthy. The sharp reduction in copper content of depleted seed suggests that these organs may reflect more sensitively the copper status of some crops than their foliage. Seeds were also relatively sensitive to changes in molybdenum status but were least sensitive to zinc.

Our results with large seeded legumes did not show the marked increase in copper content of the deficient plants reported by Millikan [11]) for the clovers, whilst the decreases in zinc content in deficient plants were generally less than those found by Millikan and were only notable in broad bean. The molybdenum content and range in dwarf bean seed compared closely with the values found by Johnson *et al.* [12]) but normal pea seeds analysed by us contained only one fourth to one sixth of the molybdenum content of commercially produced seed examined by Johnson *et al.* The data suggest that their seeds were larger as well as richer in molybdenum than ours.

SUMMARY

(1) A method is described for the production of acute deficiencies of copper, zinc or molybdenum in large scale sand cultures in which an adequate and satisfactory supply of water was obtained by treating rain water with ion-exchange resins. Results compared favourably with the use of glass distilled water.

(2) Visual symptoms of copper, zinc and molybdenum deficiencies in large seeded leguminous crops, and in other species are summarised.

(3) Seed reserves played an important part in the incidence of copper and molybdenum deficiencies and to a lesser extent of zinc deficiency in pea, runner bean, dwarf bean and broad bean.

(4) The "deficient" seed was obtained by harvesting seed from plants grown in the respective deficiency sand cultures, and was compared with seed obtained similarly from complete nutrient sand cultures or commercially from field-grown plants.

(5) Seed reserves of molybdenum were usually sufficient for a complete generation but reserves of copper and zinc were not adequate for the whole copper or zinc requirements of the plants.

(6) Analytical data showed a marked decrease in the copper or molybdenum content of "deficient" seed, and a less striking decrease in zinc.

(7) Foliage of deficient plants showed decreased content of copper and molybdenum and often of zinc compared with plants given the complete nutrient treatment, but use of "deficient" seed only decreased yields without further appreciably decreasing the mineral content of the foliage.

ACKNOWLEDGMENTS

We wish to thank Mr. G. M. Clarke, B.Sc. for statistical evaluation of the analytical data, and Mr. G. H. Jones, A.R.P.S. for the photography. The analytical method for copper and zinc was investigated and standardised by Mr. B. A. Notton whose assistance is gratefully acknowledged.

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A

B

C

Plate I

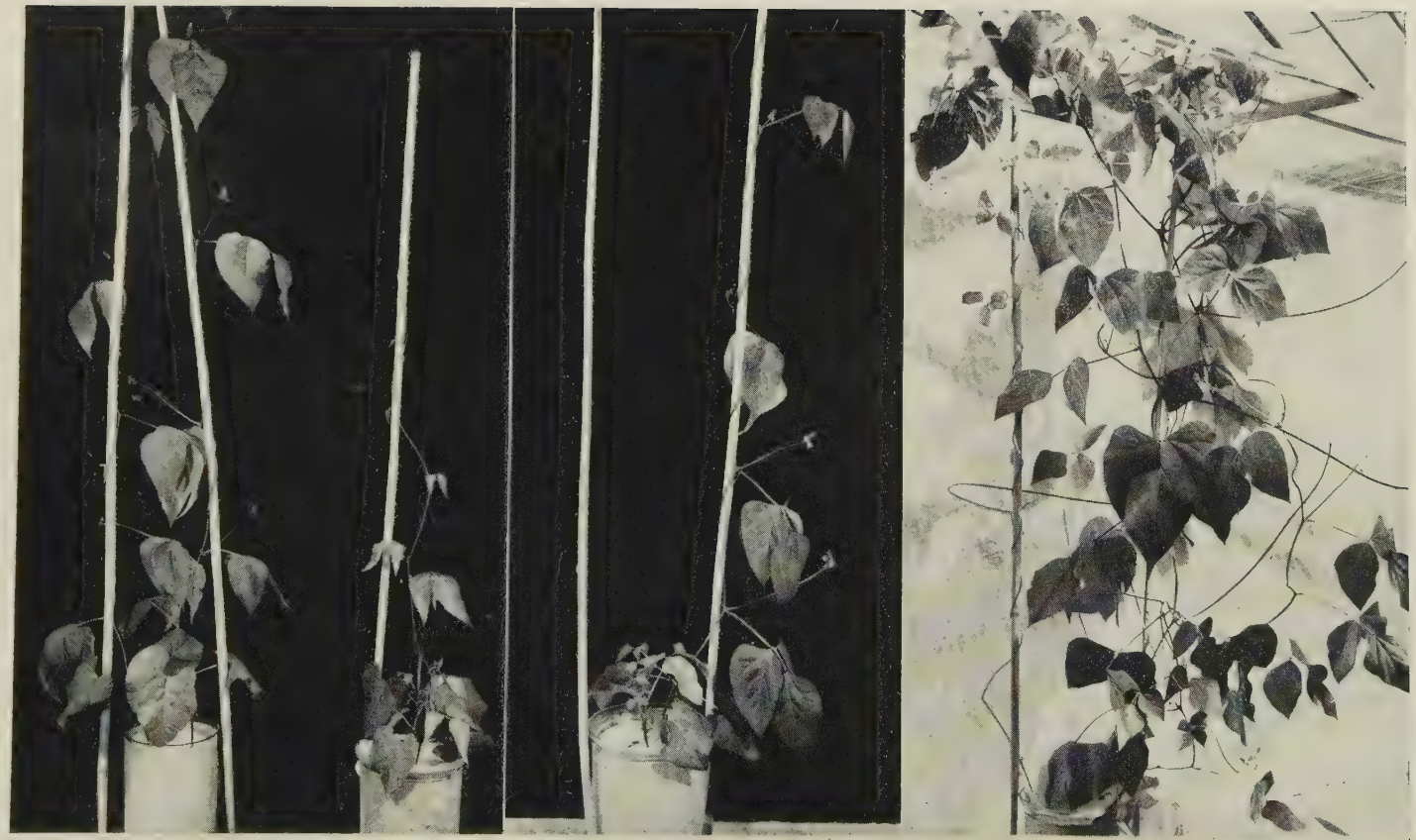

Plate III

A B C

D E

Plate IV

Plate V

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EXPLANATION OF PLATES

Plate I. Comparison of effects of different methods of water treatment on the production of copper, zinc or molybdenum deficiency in sand culture.

a. 1951 copper deficiency series in red clover; from left: complete nutrient, copper deficiency using metal distilled water, resin purified rain water, once glass- and twice glass-distilled water.

b. 1952 molybdenum deficiency series in red clover; left; complete nutrient; centre: molybdenum deficiency using resin purified rain water; right: using once glass distilled water.

c. 1952 tomato series; extreme left: complete nutrient; 1st pair: copper deficiency; 2nd pair: zinc deficiency; 3rd pair molybdenum deficiency. In each pair the pots given resin purified water are on the left and those given glass distilled water are on the right.

Plate II. Effects of seed reserves on growth of runner bean in sand cultures.

a. Left hand pot: Complete nutrient; saved seed on left, commercial seed on right. Right hand pot: zinc deficiency; commercial seed at rear slightly to left, plant climbing; saved seed at front and not climbing.

b. Copper deficiency; saved seed in front on left, plant not climbing; commercial seed at rear on right, plant climbing.

c. Molybdenum deficiency; saved seed on left, weak, chlorotic and scorched; commercial seed on right, vigorous growth.

Plate III. Copper deficiency.

a. Necrosis pattern in dwarf bean leaves.

b. Seed abortion after pod development in pea. Left hand shows apparently normal external habit of similar pods shown opened.

c. Characteristic coiling of chlorotic apical leaves of wheat.

d. Effect of seed reserves of dwarf bean. Foreground plant grown from copper deficient seed with collapse of prophylls; background plants grown from commercial seed.

e. Terminal shoot "die-back" and sudden withering from top of leaflets in lucerne.

Plate IV. Zinc deficiency symptoms.

a. Part of runner bean leaflet showing scattered rounded dark green areas in chlorotic tissue.

b. Runner bean leaflet showing pronounced marginal waving.

c. Alsike clover; pronounced marginal waving and folding of leaflets with involute leaf tips, also general chlorosis.

d. Oat; non-pathogenic lesions on older leaves showing a resemblance to manganese deficiency, plants remarkably free from mildew attack.

e. Red clover; fading and chlorotic patterns, margins of leaflets wavy (lower right from complete nutrient).

Plate V. Zinc deficiency symptoms.

a. Broad bean; characteristic conical habit, shortened internodes, narrow downcurved leaflets towards apex, and chlorosis.

b. Severe deficiency in young tomato seedlings, necrosis and collapse of first leaves.

c. "Little leaf" effect in tomato leaflets and unilateral curvature or asymmetry.

d. Coiling effect in tomato leaflets with marginal necrosis.

Plant and Soil V, no 3 August 1954

THE REMOVAL OF PLANT ROOTS FROM SOIL FOR THE ESTIMATION OF THEIR PHOSHATE CONTENT

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In the course of studies of the effect of radiation from labelled phosphate on the growth and phosphate absorption of barley seedlings it was necessary to determine the total phosphorus content of the roots and shoots of cereal plants grown in soil (Russell *et al.* [4] [5]). Consideration was given to the possible loss of phosphate from roots in the water with which they were washed. Two reasons encouraged the examination of this question: a high percentage of the phosphate in young roots appears to be present as orthophosphate ions (Heard [2]), and during other investigations in this laboratory it had been found that the removal of phosphate by solutions presented a significant problem in the preparation of tissue sections (Russell *et al.* [3]), and intact root systems, for radioautographic studies. The authors satisfied themselves that significant losses of phosphate from roots did in fact occur when the soil was removed with water, and that such losses could be reduced by the use of solutions of basic lead acetate. This information, hitherto unpublished, was communicated privately to a group of investigators engaged on similar studies at Long Ashton Experimental Station. They have recently published a statement that this treatment was without value (Bould *et al.* [1]). It appears desirable therefore to report briefly the authors' experience in this respect.

Since quantities of P^{32} exceeding 4 MC were on occasions used in a single experiment it was essential to wash the roots in such a way that the residual soil could be recovered for appropriate disposal;

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the simple procedure of placing the roots and soil in perforated metal trays under a tap in the laboratory sink could therefore not be used. The method adopted was to transfer the content of the pots from which the shoots had been harvested into hemispherical sieves of double wire gauze and support them half submerged in a bath containing water or an appropriate solution. A mechanical device caused the sieves to oscillate in a horizontal plane and the consequent movement removed the soil in approximately five minutes. After this treatment the roots were rinsed in small volumes of water. It is to be noted that the potting mixture had been passed through fine sieves (8–12 mesh) before planting, and that the pots used were small (capacity 1.5 kg soil). The procedure would not have been satisfactory if the soil had been coarse, and the handling of large volumes of soil in this way would have been tedious.

Preliminary information on the extent to which phosphate was lost from roots during this treatment was obtained by subjecting roots which had been grown in water culture to mechanical treatment comparable to that used for the removal of soil. 15.9% of the phosphate in roots thus treated in distilled water was found in the solution while the corresponding figures for roots similarly treated in 5 and 15% basic lead acetate solutions were 5.4 and 2.0% respectively.

The effect of treating plants grown in soil with 15% basic lead acetate was then investigated. The shoots of plants in replicated pots from five treatments of an experiment were removed at ground level and the pots were divided into two groups one of which was treated with 200 ml 15% lead acetate solution per kg soil while the other received no such treatment. This volume of lead acetate solution was considered adequate since the lead content of the final leachings was only slightly less than that of the original solution. Twenty-four hours later the roots were washed free of soil and assayed. The phosphate content of roots from pots which had not been treated with lead acetate was 82.5% of that of those which had been treated (5%, fiducial limit: $\pm$ 6.2). The lead acetate treatment was consequently adopted as a routine measure.

The authors have no knowledge of the experiments which led Bould and his colleagues to reject this procedure apart from their brief published statement (Bould *et al.*, *loc. cit.*). No explanation of the divergent experiences in the two laboratories can be offered.

It is obvious however that many factors will affect the extent to which the lead acetate treatment reduces the loss of phosphate from roots. It appears reasonable to assume that when no precautions are taken the major loss of phosphate will occur from the finer roots since they suffer the greatest mechanical injury. Thus the value of the lead acetate treatment may depend on the efficiency with which the roots are recovered.

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MANURING, PLANT PRODUCTION AND THE CHEMICAL COMPOSITION OF THE PLANT

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When a crop is manured — manuring in the widest sense of the word and including for example light, temperature, humidity, *etc.* — the production of dry matter per unit area and the chemical composition of the dry matter are influenced. It is characteristic that both the total production and the various elements and compounds involved in this production are influenced. This means that the connection between the dry matter production, the production of protein, amino acids, vegetable oil, starch, sugar, fibres, absorption of various macro and micro elements, *etc.*, and the manuring is a rigid one in each special case.

The purpose of much work done during the last century has been to formulate general rules for the above-mentioned relationships. If such formulations are possible they may be used for various practical purposes.

The principal relationships may be expressed graphically, the units of the abscissa representing the amounts of manure added, the ordinate expressing the production of dry matter, and both values being expressed in terms of weight per unit area. All similar relationships which may be of interest are in one way or another derived from or related to this curve which will subsequently be called the yield curve. The yield curve may be extended to comprise coordinate systems with more than two axes.

THE VARIATION IN AND POSITION OF THE YIELD CURVE

The primary importance of the yield curve in all investigations of the above-mentioned kind has been appreciated at various times.

It is generally agreed to-day that mathematical expressions for the yield curve may be useful in a variety of ways. On the other hand knowledge of the fundamental factors influencing the yield curve cannot be obtained by mathematics, but only by well performed experiments, the design of which is in accordance with existing knowledge so that the results may throw further light on the yield curve and related matters. This may seem a superfluous statement, but it is justified by experiences which show that the design of many experiments and interpretation of the results of these experiments do not throw much light either on fundamental or on practical aspects of the problem, possibly because many of the investigations have been made for purely practical purposes.

When examining variations in the yield curve it is essential that determinations are made of the production of dry matter and the amount, or amounts, absorbed of those plant nutrients which are, or may become limiting — both expressed as quantities per unit area. — That such fundamental investigations must be made in this way is apparent from Figures 1, 2 and 3, in which the scale of the units of the abscissae and of the ordinates are the same in all three figures. These figures are more or less diagrammatic; details of the design of the experiments and the experimental results may be obtained from the following papers: Russel and Watson [15]), Hellriegel and Wilfarth [6]), Mitscherlich [12]), Wallace [26] [27] [28] [29]), Kristensen [9]), Steenbjerg [17] [18] [19] [20] [21] [22] [23] [24]), Poulsen [14]), Jacobsen [7]), Jakobsen [8]), Goodall and Gregory [3]), Brown and Harmer [2]), Haddock [4] [5]), Boken [1]). These citations are made with particular reference to papers from this institute.

Figure 1 shows the relationship between the addition of increasing amounts of a plant nutrient, l, which is present in limiting quantities and the production of dry matter. Figure 2 shows the ratio between the amount added, l, and the amount absorbed, o, of this nutrient. The form of this curve may be altered by determination of coefficients of absorption of the nutrient in question by means of radioactive isotopes; this may alter some of the following conclusions with respect to the ease with which variation in the curve is observed, but will not alter the general shape of the yield curve in Fig. 3. Fig. 3 shows the relationship between the amount absorbed, o, of a plant nutrient present in limiting quantity and the production of dry

matter. All yields, amounts of nutrients or amounts of nutrients added in Figs. 1, 2 and 3 are expressed in terms of weight per unit area. These three relationships are of fundamental importance.

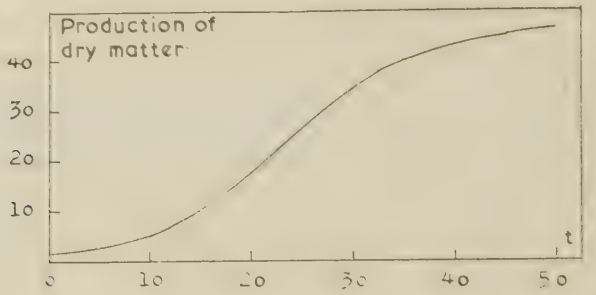

Fig 1

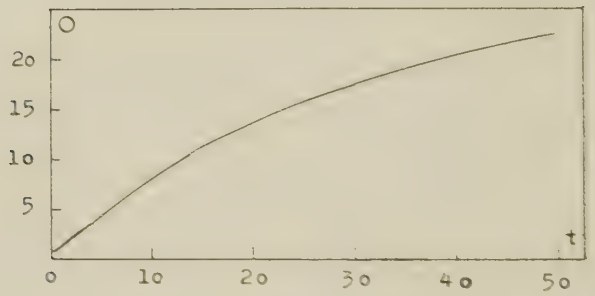

Fig.2

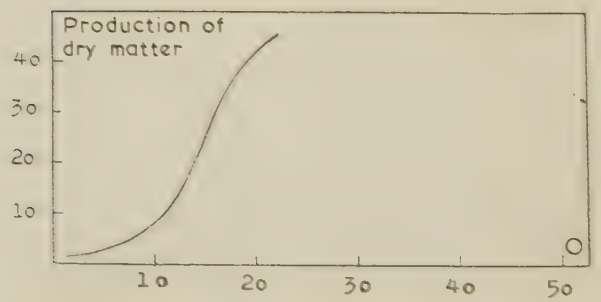

Fig. 3

Fig. 1. The relationship between *t* and the production of dry matter.
Fig. 2. The relationship between *t* and *o*.
Fig. 3. The relationship between *o* and the production of dry matter

Fig. 3 is easily derived from Fig. 1; this has been done graphically through Fig. 2; the relationship represented in Fig. 2 may be determined by chemical methods.

The method of examining the form of the yield curve in Fig. 3 has two advantages, which so far seem to have been overlooked. The S-shape of the curve may be difficult to observe in Fig. 1, but as the coefficient of absorption falls with rising x values it is evident that the concave part of the yield curve will be easier to observe in Fig. 3 than in Fig. 1. This method of investigating the shape of the curve has also the great advantage that one end of this yield curve coincides with the zero point of intersection of the axes. This point is therefore fixed and is extremely useful in the extrapolation and interpolation of experimental data for decreasing values of o and dry matter.

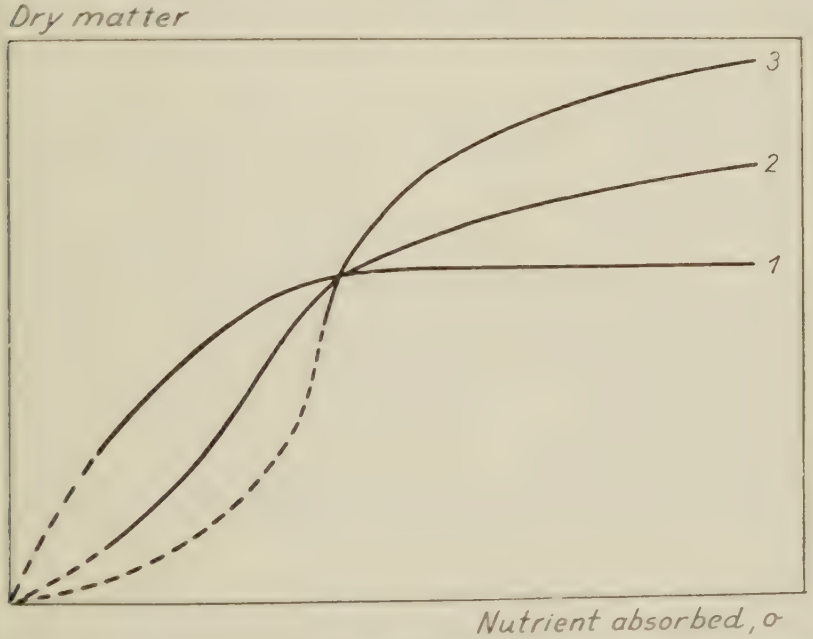

Fig. 4. The relationship between the amount of nutrient present in limiting quantity, absorbed and the production of dry matter.

Fig. 4 shows a schematic graphic representation of a long series of experimental results, mainly from this institute and from a few other papers, mainly Danish, where it has been possible to compute the

amounts absorbed of the nutrient present in limiting quantity. The parts of the curves shown as an unbroken line are based on experimental results, while the parts of the curves shown as dotted lines represent interpolations to the zero point of intersection of the axes. The three types of yield curves (1, 2 and 3) in Fig. 4 must all have one end in, or very near, the zero point of the axes because production of dry matter without absorption of the plant nutrient present in limiting quantity as well as absorption of this nutrient without production of dry matter are equally inconceivable from a physiological point of view and, when apparently observed when the crop is harvested (because of observational errors), might give rise to strange deductions, indeed.

At present the following considerations seem useful when considering whether experiments have been carried out under conditions such that the S-shape of the yield curve may be observed; awareness of these criteria may be useful when smoothing the experimental results.

1. For the same plant, the lower the yield from the basic experimental treatment, the higher the probability of an S-shaped curve being observed.

2. If a very marked deficiency of the plant nutrient in question occurs in the basic treatment, then the amount of tissue imparting rigidity to the stem in gramineae generally seems to be very low, often so low that it may be detected by handling.

3. The observation of typical and widespread symptoms of deficiency of the plant nutrient present in limiting quantity in all replications receiving basic treatment make it probable that the curve should be S-shaped.

4. If the experimental results could be represented graphically as in Fig. 3, this would be very advantageous, as mentioned above.

For further details regarding the conditions governing the shape of the yield curve and its position in the coordinate system the following papers may be consulted: [17]) [18]) [19]) [20]) [21]) [22]) [23]).

To prevent any misunderstanding it may be necessary to emphasize here that the S-shaped curve or parts of S-shaped curves have often been observed in well performed experiments concerning all the ordinary nutrients.

In what follows a few consequences of the S-shaped curve are

considered; several more consequences easily present themselves, but will not be discussed here.

We shall first consider the results from two experiments, *1)* a field experiment with nitrogen (nitrate) in limiting quantity, and *2)* a pot experiment with copper in limiting quantity. The results from the experiment with nitrogen have been selected to show, among other things that even for a major nutrient, such as nitrogen, S-shaped curves may be observed when the results are obtained from a long term experiment where the soil, in the basic treatment and in one or two of the treatments where small amounts of nitrogen have been added, is more or less depleted of this nutrient.

In the field experiment (Fig. 5*a*) with nitrogen only the convex part of the yield curve is obtained; but it is clearly seen that the curve is actually S-shaped when the curve is extrapolated to the zero point of intersection of the axes. On the other hand, in the pot experiment, where copper is present in limiting quantity, nearly the whole of the yield curve is observed; and it is seen to be S-shaped. Figs. 5*a* and 6*a* show the relationship between the dry matter production per ha or per pot, and the amounts of nitrogen and copper absorbed, respectively. Figs. 5*b* and 6*b* show relationship between content of nitrogen (%), content of copper (ppm) and dry matter production.

Dry matter production plotted as the abscissa may be replaced by any other related factor, *e.g.* the corresponding amount of added nitrogen (when this is a limiting factor), starch production, vegetable oil production, protein production, or whatever factor is of interest. It may be added here that if the slope of the yield curve in question decreases when very large amounts of the nutrient present in limiting quantity are added (increasing negative increments of *e.g.* dry matter), then the case is further complicated and will not be considered here.

Some of the consequences of these observations of S-shaped curves or parts of curves, which are essentially parts of S-shaped curves, are exemplified in Figs. 5*a*, 6*a*, 5*b*, and 6*b*. The first example is chosen because it shows how important it is to consider both the possible shape of the yield curve, which so far has been discussed most in the present paper, and its position in the coordinate system. The use of chemical analyses of nutrient elements in plants or parts of plants as an index of the nutritional status of these plants has

been much advocated in recent years. The purpose of such analyses is to make possible recommendations regarding manurial treatments

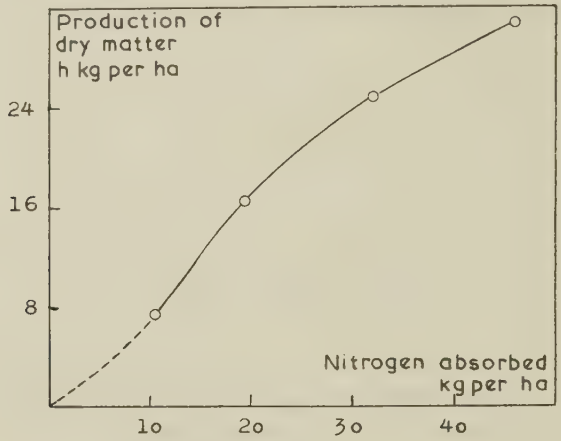

Fig.5a

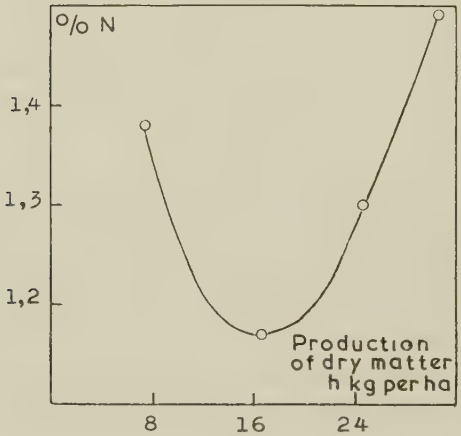

Fig.5b

Fig. 5*a*. The relationship between nitrogen absorbed and the production of dry matter. Timothy. Leaves + straw. — Tylstrup 1931–42.
Fig. 5*b*. The relationship between the production of dry matter and the content of nitrogen as a percentage of the dry matter. Timothy. Leaves + straw. — Tylstrup 1931–42.

on either a qualitative or a quantitative basis. These recommendations may be derived from appropriate field experiments the results of which are analysed statistically, primarily with respect to the

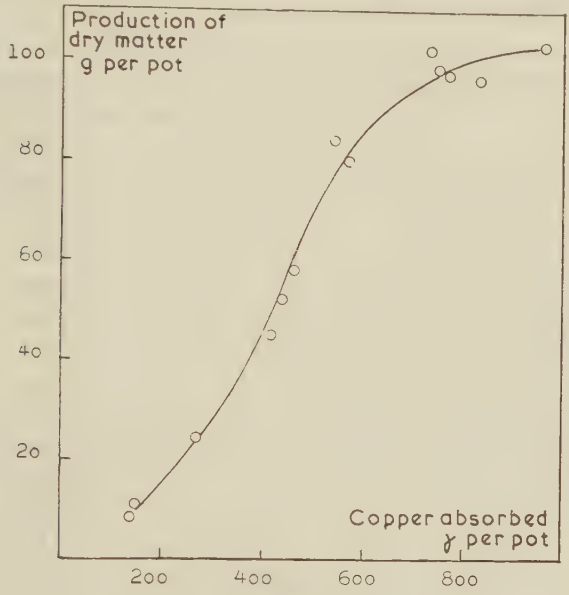

Fig. 6a

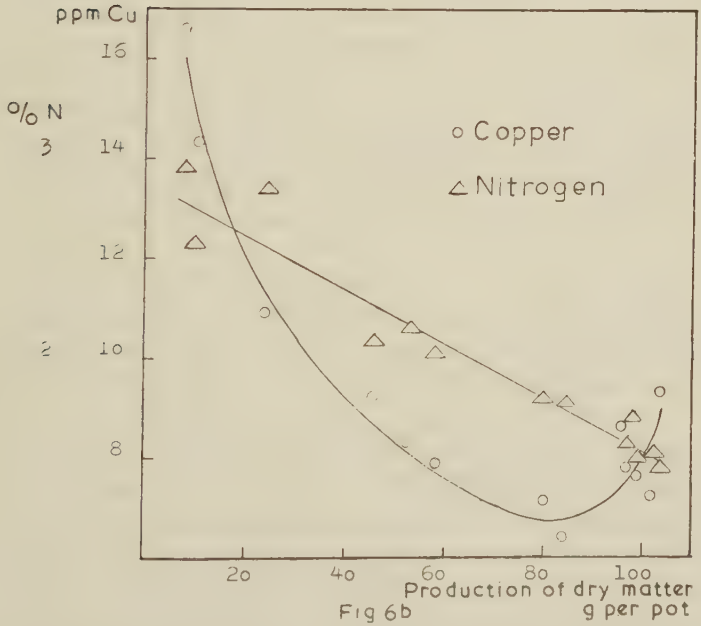

Fig 6b

Fig. 6*a*. The relationship between copper absorbed and the production of dry matter. Barley. Leaves + straw. — Copenhagen, 1939–41.

Fig. 6*b*. The relationship between the production of dry matter and the relative content of copper (ppm) and nitrogen (%). Dry matter basis. Barley. Leaves + straw. — Copenhagen 1939–41.

nutrient present in limiting concentration, but also with regard to other factors of production, which are most important in connection with the form and position of the yield curve [23]). A special method of statistical treatment (verification) is met with in the so called spot or patch investigation, a method of special value in all cases in which few results from field experiments are available for verification of the results of the chemical analyses. At least three samples of plant material (the whole plant or parts of it according to preceding investigations) are taken from healthy, less healthy, and deficient crops (Figs. 5*a* and 6*a*), and the contents of the most important plant nutrients are determined.

When taking samples of material for analyses care must be taken to choose such organs of the plants (or the whole plants) that the differences in the analytical results will be as great as possible. The same care is necessary when choosing analytical methods and agents used for extraction. The determination of the total percentage content of a nutrient in the dry matter — and this must be considered the standard method — may be used to obtain this maximum variation, while in the case of a few elements, such as for example nitrogen, fractionation into the various forms such as total nitrogen and nitrate nitrogen *etc.*, may often be used with advantage (Ulrich [25]), Haddock [4] [5])). However, very few results are available which allow of a comparison between the values of these fractions and the values of total contents (Jacobsen [7])). Finally, the sampling should be carried out during that part of the growing season when differences in the analytical results will be greatest; in temperate climates this means the early summer, *i.e.* May and June. In this connection it is suggestive that the most pronounced and widespread symptoms of deficiency are generally found in the above-mentioned early periods of growth.

The interpretation of the results when using this method of sampling is based on the assumption that by sampling simultaneously and with as small distances as possible all factors influencing the shape and position of the yield curve, except the one limiting growth, are kept constant or as nearly so as possible at the places of sampling. This means that when sampling, distances in time and space must necessarily be very small. It is of vital importance that this elimination of variables be successfully carried out when sampling, as otherwise one may inadvertently measure simultaneously the influence of two or more factors on the yield curve and on the percentage content of for example one of the nutrient elements. How complicated and how difficult the interpretation

may be in apparently rather simple cases is exemplified in the diagrams in Figs. 7*a* and 7*b*; here more than one factor of production has been varied simultaneously in the three sampling sites for both the first and the second sampling.

By simultaneous sampling on patches separated by distances as small as possible one ensures, as far as possible, that the varying yields corresponding to the samples taken, originate from one yield curve and not from three curves as in Fig. 7*a*. This simplifies the interpretation of the results originating from spot investigations because one only needs to pay special attention to the shape of the yield curve; but even in this case the interpretation may be difficult. It is important that a series of measurements is secured, the graphic representation of which resembles Figs. 5*b* and 6*b*. Furthermore, it is necessary to analyse the plant samples for several elements, not only the one which may be in limiting quantity. When present in sufficient quantities the percentage contents of the nutrients not present in limiting concentration will, on the whole, show a constant decrease with increasing weight of dry matter of the crop. On the other hand, the nutrient present in limiting concentration shows first a decrease and then an increase in percentage content with increasing amount of dry-matter production. If samples of such crops are obtained for chemical analysis, the information on the yield and the appearance of deficiency symptoms may be lacking or inaccurate; hence it may be necessary to analyse the crop not only for the plant nutrient present in limiting concentration but also for a number of other plant nutrients (Fig. 6*b*).

On the whole it seems necessary to use chemical analyses of plant material with caution and some reservation as a diagnostic criterion of deficiency of soils and crops in plant nutrients. Such analyses should never be used alone, but always in conjunction with other independent methods of observation (compare Lundegardh [10]) [11]).

The second example shows some other consequences of the S-shaped yield curve; it is chosen because it demonstrates how careful one must be when selecting plant material for chemical analyses with respect to percentage content of various important constituents in the crop on a dry-matter basis. In the experiment with nitrogen (Fig. 5*b*) it is seen that the percentage content of crude protein may be exactly the same in two crops which are very differ-

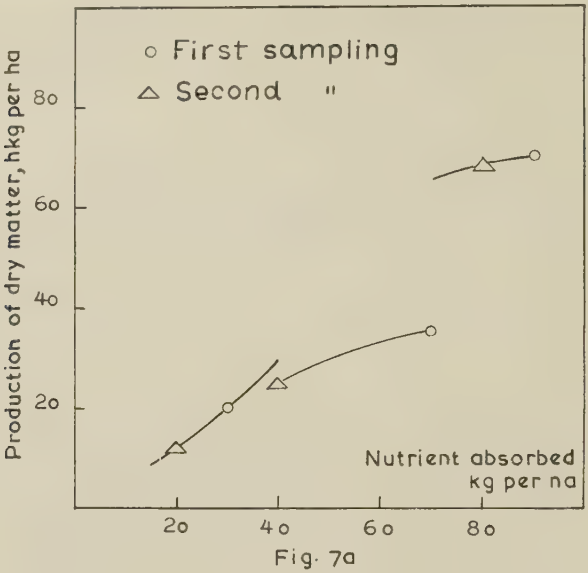

Fig. 7a

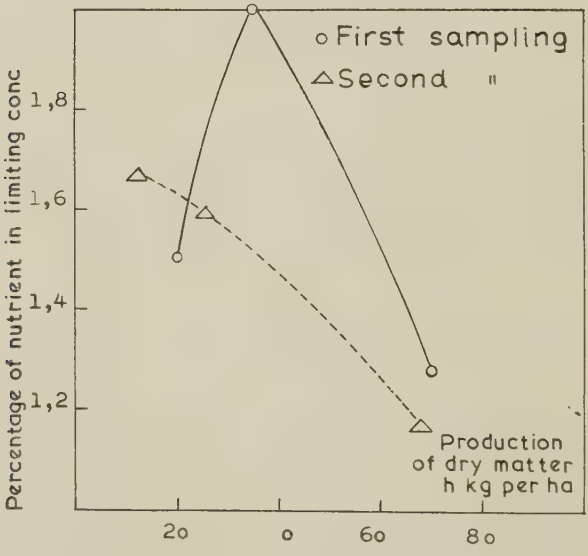

Fig. 7b

Fig. 7*a*. The relationship between the nutrient absorbed (present in limiting concentration under various circumstances with respect to other nutrients) and the production of dry matter.

Fig. 7*b*. The relationship between the production of dry matter and the percentage content of the nutrient present in limiting concentration (under various circumstances with respect to other nutrients).

ent in the amount of dry matter produced. Thus in a field experiment in which increasing amounts of nitrogen are added to the soil, and the experiment includes only a few experimental treatments, one may by accident sample crops which show no variation or only a very small variation in the percentage content of crude protein with increasing addition of nitrogen to the soil and increasing crop production; one may even find decreasing nitrogen content with increasing nitrogen addition to the soil.

The same picture of the influence of nitrogen fertilisation may be obtained for other nitrogenous compounds found in the plant. Therefore, when using plant material for chemical analysis from long-term field experiments in which the soil in the basic treatment is generally more or less depleted of nitrogen, one must be careful. Many surprisingly small variations of the above-mentioned kind may have been caused by an underlying S-shaped yield curve for dry-matter production.

In this connection it should be mentioned that the computed yield curve for crude protein is S-shaped when calculated on the basis of Fig. 5*a* and Fig. 5*b*, but the very same is true of the yield curve for crude protein (Fig. 8) when computed on the basis of Fig. 6*a* and Fig. 6*b*. These facts are rather important and open up new fields for further research.

Furthermore, the above-mentioned facts mean, among other things that proportions of percentage contents, *e.g.* $\frac{\text{ppm Cu}}{\%\ \text{N}}$ or $\frac{\%\ \text{N}}{\%\ \text{P}}$, *etc.* in the above-mentioned examples are of small importance for the verification of chemical plant analyses or tissue tests.

The third example is chosen to show that the shape and position of the yield curve is most important in determining the most beneficial distribution of a given amount of a nutrient element which is present in limiting concentration on a given area. The most beneficial distribution is defined as that which for a given amount of a fertilizer, gives the highest yield per unit area.

When trying to determine which method of distribution is most beneficial it must be remembered that several experiments with different plant nutrients in various parts of the world have shown that uneven distribution of fertilizers, *e.g.* in rows, or otherwise have in some cases given enormously higher yields than an even distribution on the surface of the soil. The causes are different in different cases and in fact are not known precisely.

The explanation may lie in the fact that some soils, often, but not always, soils depleted of the nutrient in question, have a very high fixing power for the nutrient, making it difficult for the plants to absorb it. This may be one of the causes of the concave part of the yield curve.

In such cases, instead of choosing an uneven distribution of a given amount of the nutrient on a given area of soil, the fertilizer, if watersoluble, may — as shown by much research work — with great economy of material be sprayed in small concentrations on the leaves, twigs, branches, *etc.*, of the plants once or several times during the growing period or at other times of the year.

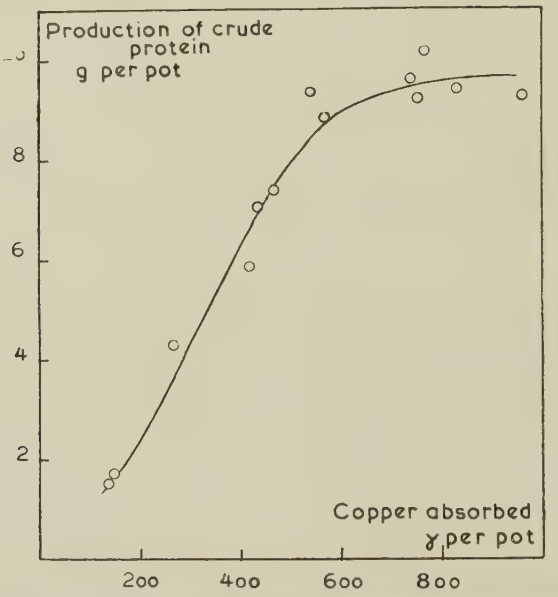

Fig. 8. The relationship between the copper absorbed and the production of crude protein. Barley. Leaves + straw. — Copenhagen 1939–41.

The consideration governing the choice of an uneven distribution of a given amount of nutrient to the soil seems to be that the underlying yield curve represents the lower part of the curve, part of which is concave.

Under many conditions, however, it may often pay to manure in such a way that the yield level lies on the upper part of the curve. This means that more nutrient must be brought into circulation in the field when conditions of production allow this. In this connection it should also be remembered that an uneven distribution does not last in a soil which is ploughed, *etc.*, at regular intervals.

Simple considerations will show:

1. That when a given amount of the fertilizer in question is broadcast and distributed as evenly as possible on a given unit of area, *e.g.* 1 ha, any other distribution of the same amount of fertilizer on the same area will provide exactly the same yield per ha if the yield curve is a straight line.

2. That when a given amount of the fertilizer in question is broadcast and distributed as evenly as possible on a unit area *e.g.* 1 ha, the highest yield will be obtained from this kind of distribution when the underlying part of the yield curve is convex.

3. When forced to work on the lower part of the yield curve part of which is concave, the highest yield will be obtained by an uneven distribution. The degree of unevenness of distribution depends on the shape and position of the yield curve.

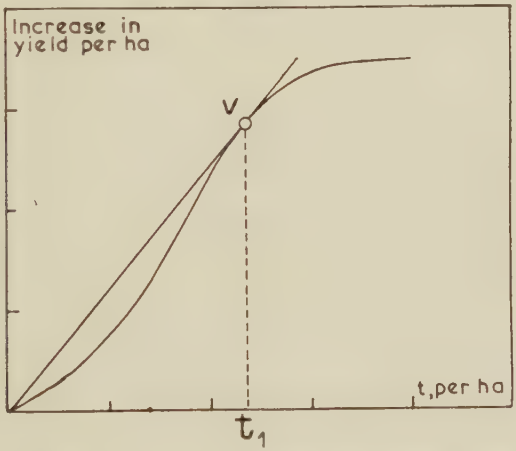

Fig. 9. The relationship between the nutrient added, t and the increase in yield.

In Fig. 9 is a diagrammatic representation which shows a tangent at the point, v, extended through the zero point of intersection of the coordinate axes. The reciprocal t_1-value in Fig. 9 gives that part of 1 ha on which one unit of a fertilizer must be spread evenly in order that the highest yield is obtained per ha (compare de Wit [31]). Instead of absolute values relative values for fertilizers may be used.

An example illustrating this is given below: An experiment in which increasing amounts of a fertilizer have been used has been performed, and the fertilizer in question has been spread as evenly as possible. Table I gives the results:

TABLE I

Units of fertilizers added/ha	Total increase in yield/ha	Yield increments	Increase in yield per unit of fertilizer/ha
1	1.5	1.5	1.50
2	4.0	2.5	2.00
3	8.0	**4.0**	2.67
4	11.7	3.7	**2.93**
5	14.2	2.5	2.84
6	15.9	1.7	2.65

The largest increase in yield per unit of fertilizer per ha is obtained on addition of 4 units of fertilizer per ha. If only 1 unit of the fertilizer is available for use the largest increase in yield per ha will be obtained by spreading it on $^1/_4$ of a ha; if 2 units of a fertilizer are obtainable they should be spread on the half of 1 ha and spread as evenly as possible on this half ha as mentioned above. If more than 4 units of the fertilizer are available per ha the fertilizer should be spread as evenly as possible over the whole of the area.

The increase in yield per unit of fertilizer per ha is equal to the average value of the preceeding yield increments *e.g.* for 4 units of the fertilizer: $1.5 + 2.5 + 4.0 + 3.7 = 11.7$, $11.7 : 4 = 2.93$. This is the reason for the maximum increase in yield per unit of the fertilizer per ha not coinciding completely with the maximum yield increment which in this example is found when 3 units of the fertilizer are applied per ha and which marks the point of inflexion of the curve.

As long as the yield increment is larger than the average value of the preceeding yield increments the increase in yield per unit of the fertilizer per ha increases and vice versa.

An uneven distribution of a fertilizer is dictated by the necessity for working on the lower part of the yield curve — for economical reasons and/or lack of the necessary fertilizers in such amounts as would raise the yield to that point of the curve where the highest net result may ordinarily be obtained.

SUMMARY

The paper deals with some of the consequences of an S-shaped yield curve with special reference 1) to the chemical composition of the plant and 2) to the distribution of fertilizers.

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Plant and Soil V, no 3 August 1954

THE PHOSPHATE STATUS OF GARDEN SOILS IN RELATION TO SOIL pH

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It is well known that soil pH exerts an important effect on the availability to plants of the phosphate present in the soil. Numerous studies have shown that, in general, acid soils are likely to be low in available phosphate because of the ability of iron and aluminium, which tend to come into solution in acid soils, to react with soluble phosphate so as to "fix" it in forms which are unavailable to plants. In slightly alkaline or calcareous soils there is also a certain tendency for phosphate to be rendered unavailable through formation of complex calcium compounds. The optimum pH level for high phosphate availability has been shown to occur in neutral or slightly acid soils.

This paper presents the relation between phosphate availability, as determined by a chemical method, and pH of 800 garden soils*) examined in routine advisory work over a period of four years. The soils, representing all textural classes, originated from various parts of the United Kingdom, although the bulk of them came from England. Greenhouse soils and obviously peaty soils, such as the fenland types, are not included in this survey.

PROCEDURE

The soil samples were air-dried and ground to pass a 2 mm sieve. pH was determined with the B.D.H. soil testing outfit. The pH of the soils are given to the nearest 0.5 of a pH unit, so that a soil designated as having a pH of 6.5, for instance, may fall in the approximate range 6.2 6.7. Available phosphate was determined by a "rapid" chemical test, using the Morgan extraction technique [1]) as modified by Tinsley and Pizer [2]). The significance of the phosphate fertility levels "low", "medium", "high", and "very high" may be defined broadly as follows:

Low	Soil very likely to respond to phosphate fertilisation.
Medium	Soil may or may not respond to phosphate fertilisation.
High	Soil unlikely to respond to phosphate fertilisation.
Very high	Soil very unlikely to respond to phosphate fertilisation.

*) Acknowledgment: The author is indebted to the Director of the Royal Horticultural Society Gardens and Members of the Royal Horticultural Society for the soil samples,

RESULTS

The phosphate status of the 800 soils examined in relation to soil pH is shown in Table I.

A study of this table shows that the soils may be divided broadly into three groups with regard to their likely response to phosphate fertilisers:

TABLE I

Phosphate status of soils of different pH. Each value in the body of the table represents the *percentage* of soils in each pH group having a given phosphate status, *e.g.*, the value 13 in the top left hand corner indicates that 13% of the 153 soils of pH 8 examined had a "very high" phosphate status
(Note: the percentages have been rounded off)

Phosphate status	Soil pH						
	8	7.5	7	6.5	6	5.5	5
	Number of Soils examined						
	153	170	134	84	114	125	20
	%	%	%	%	%	%	%
Very high . . .	13	12	19	11	2	1	0
High	50	53	55	37	23	10	0
Medium	19	18	9	23	29	15	5
Low	18	17	17	29	46	74	95

(*a*) Soils of pH 5 and 5.5 (fairly and moderately acid soils), of which the bulk are very likely to respond to phosphate fertilisation.

(*b*) Soils of pH 7 to 8 (neutral and alkaline soils) of which the bulk are unlikely to respond to phosphate fertilisation.

(*c*) Soils of pH 6 and 6.5 (slightly and very slightly acid soils), in which the availability of phosphate is fairly uniformly spread over the whole fertility range.

Certain trends are apparent from a study of the figures in the table. Soils of "low" phosphate status make up only 17–18% of the soils in the pH range 7–8. As the pH falls from 7, so the percentage of soils in this category increases rapidly to 95% at pH 5. Soils of "high" (including "very high") phosphate status show a trend in the reverse direction, namely, a high percentage at pH 7–8, followed by a rapid drop in percentage as the pH falls.

It is interesting to note that the percentage of soils in the "high" + "very high" group is at a maximum for soils of pH 7 (74% of the soils in this pH group).

DISCUSSION

The fact that 11–19% of the soils of pH 6.5 or greater have a "very high" phosphate status confirms the general observation that many garden soils are over-manured with respect to phosphate fertilisers. The very small percentage of soils of pH 6 or less in this group indicates that titration processes have probably been active in this pH range.

It is well known that soils bearing ericaceous plants must of necessity be maintained at low pH. The author has noted a number of cases where rhododendrons and azaleas have been thriving on soils of low pH (5.5 or less) having a "low" phosphate status as determined by the Morgan method. This appears to cast certain doubts on the real value of the Morgan method in estimating phosphate availability with respect to ericaceous plants in such acid soils. It is likely that for these soils and plants the stronger reagents such as 1% citric acid, which are capable of dissolving forms of phosphate not dissolved by the Morgan reagent, may be of more value in indicating their true phosphate status. It must be pointed out, however, that the Morgan method is a "safe" method of determining phosphate availability in acid soils, in that, whereas it may indicate a "low" phosphate status in soils which are in fact able to supply sufficient phosphate to plants, it is unlikely to indicate a "high" phosphate status in soils which are not in fact able to supply sufficient phosphate to plants.

SUMMARY

The phosphate status of 600 garden soils, obtained from various parts of the United Kingdom, as determined by the Morgan extraction method is presented in relation to soil pH.

74%–95% of the soils of pH 5 to 5.5, 29%–46% of the soils of pH 6 to 6.5 and 11%–19% of the soils of pH 7 to 8 had a "low" phosphate status.

11%–19% of the soils of pH 6.5 to 8 had a "very high" phosphate status, indicating over-manuring with respect to phosphate fertilisers.

There are indications that the Morgan method is not entirely satisfactory for determining phosphate availability in soils of pH 5.5 or less.

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EFFECT OF MINERAL NUTRITION ON LODGING OF CEREALS

by E. G. MULDER *)

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1. Introduction.
2. Experimental methods.
3. Plant characters related to tendency to lodging.
4. Effect of nitrogen nutrition on lodging and on plant characters related to tendency to lodging.
5. Effect of potassium nutrition.
6. Effect of phosphorus nutrition.
7. Effect of soil-pH.
8. Effect of soil structure.
9. Effect of lodging on yield.
10. Discussion.
11. Summary.

1. INTRODUCTION

In the course of an investigation into the effect of nitrogenous fertilisers on the growth and yield of cereal crops, it was observed that lodging is often the limiting factor in attaining maximal yields by increased nitrogen supply. This is particularly the case under the humid conditions prevailing in the Netherlands during the greater part of the growing season of the cereals. Although for the production of high grain yields some bending over of the ripe plants is desirable, severe lodging both from the point of view of grain formation and of harvesting is unprofitable.

In order to learn the circumstances under which lodging occurs, a number of field and pot experiments with rye, wheat, barley and oats have been carried out from 1940 to 1949. In most of the field experiments nitrogen dressings have been combined with applications of other nutrients and with variations in rate of seeding and in spacing.

Although many papers have dealt with the problem of lodging, there is considerable disagreement amongst various authors as to its cause. The first investigators who studied this phenomenon came to the conclusion

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that lack of silicic acid was responsible for the inadequate standing ability of cereal plants (see Święcicki[34])). Although the view that lodging has to be ascribed to an inadequate uptake of silicic acid may be found in a number of subsequent papers, the fact that normal cereal plants could be cultivated in nutrient solutions from which silicic acid was withheld made it clear that the Si-deficiency hypothesis was untenable.

Sachs[31]), Koch[22]) and many other investigators have associated tendency to lodging with etiolation of the lower internodes of the stem as a result of a high rate of seeding or high fertility, particularly abundant nitrogen. The long and weak lower internodes which resulted would have little resistance to bending as a result of which lodging of the crop would easily occur.

Kraus[24]) who has made a very comprehensive study of lodging phenomena in cereals, admits that etiolation of the lower internodes makes the culm more liable to bending, and therefore has to be considered an important factor in causing tendency to lodging; he denies, however, that lodging occurs simply as a result of etiolation. Plants with strong stems may also lodge when their root development or the anchorage of the roots in the soil is inadequate. The view of Kraus concerning the importance of a well-developed root system in lodging-resistant plants is also found in some more recent papers. Caffrey and Carroll[8]) who have investigated a number of oat varieties for various characters related to tendency to lodging came to the conclusion that a large proportion of well-developed, strong, unbranched anchor roots extending horizontally through the soil may provide the best possible anchorage for the plants. In addition to such a root system, lodging-resistant plants should have sturdy lower stems.

The view that both strength of straw and development and anchorage in the soil of the root system are important factors in procuring a strong standing ability of cereal crops is found in a number of papers (Hanley[20]) Halliday[18]), Hamilton[19])). The latter has made a comprehensive study of the root development of eight oat varieties possessing a different degree of lodging resistance. Varieties with a high degree of resistance were generally found to produce large, widely spreading and rigid coronal roots. Varieties which lodged easily were found to possess smaller and more flexible roots, which had a greater tendency to grow downward in the soil. It is difficult, however, to decide to what extent the resistance to lodging of these oat varieties has to be attributed to the development of their root systems since the latter was found to be significantly correlated with the diameters of the lower parts of the culms.

Many authors have investigated resistance to lodging in connection with the breeding of new varieties of cereals. They have studied various plant characters in relation to resistance to lodging with the purpose of making use of these characters in isolating varieties with a high standing ability. This is of particular importance to those breeders who are working in regions where lodging does not occur regularly. There is, however, decided disagreement between various authors as to the relative importance of various plant characters as an index for lodging resistance. This is largely due to

the fact that a considerable amount of the variation in these characters found in a population of different strains has to be ascribed to environmental influences. Apparently the intervarietal differences between most plant characters related to lodging resistance have only a relative value. When the growing conditions have been changed these differences also may undergo considerable change. Brady [6]) measured a number of plant characters of three oat varieties differing in resistance to lodging. It was found that the variety having the greatest standing ability had the shortest lower internodes, the thickest fifth internode, the thickest culm wall, the greatest number of vascular bundles, the greatest thickness of thick-walled tissue and the thickest sclerenchyma cell walls. Although these findings may demonstrate the importance of many attributes in strengthening the culm of oat plants, according to Brady, these characters cannot be used as an absolute index for lodging resistance since they appear to be variable under the influence of various growing conditions. In agreement with Garber and Olsen [12]) the thickness of the sclerenchyma cell walls was found to be the most independent of soil variations. Even this characteristic, however, was considered too unstable a factor to be of use as an absolute criterion of the lodging-resistant ability of a variety.

According to Salmon [32]) breaking strength of the straw may be used as an index for resistance to lodging. It would be even a better measure of tendency to lodging than lodging itself since the latter is closely related to the occurrence of adverse weather conditions. Davis and Stanton [10]) found a relatively good agreement between standing ability of oat varieties in the field and breaking strength of the straw. Clark and Wilson [9]), however, were unable to find a correlation between lodging index and breaking strength of the culms in field experiments including 24 varieties of summer wheat and 17 varieties of barley. They obtained a significant correlation between diameter of culm and breaking strength. Atkins [2]) [3]) found no significant correlation between lodging and breaking strength of the straw. Nevertheless he believed that breaking strength determinations can be used to predict lodging behavior in the field and consequently can be used in a breeding programme to isolate lodging-resistant strains. Breaking strength of the straw was found to be closely correlated with culm diameter and with weight per unit length of culm at the base of the plants in wheat. Since the latter can be determined more easily than breaking strength, this author substituted weight per unit length of culm for breaking strength determinations as a measure of lodging resistance. Van Dobben [37]) obtained a poor correlation between weight of basal culm and lodging resistance of a number of varieties of barley, oats and wheat.

Albrecht [1]) found no correlation between breaking strength of the straw and length of the internodes in wheat plants. The former was found to be positively correlated with culm diameter, weight per unit length of culm and wall thickness of the culms. The positive correlation between strength of straw and thickness of sclerenchymatous ring was much less close than that between strength of straw and development of vascular

bundles. Culm wall thickness and relative development of vascular bundles were considered by this author to be the most important attributes in connection with resistance to lodging. According to Moldenhawer [25]) lodging-resistant varieties of wheat have a greater number of vascular bundles than varieties which lodge easily. This does not agree with the results obtained by Caffrey and Carroll who found more vascular bundles in an oat variety which was very liable to lodge than in one which had a high resistance to it. Hamilton [19]) found the greatest number and size of vascular bundles in lodging-resistant oat varieties.

Welton [38]) and Welton and Morris [39]) ascribe lodging to a low weight of dry matter per unit length of culm. This may result from a relatively low content of lignin and other carbohydrates and a high water content or from the development of slender culms. According to Hamilton [19]) a lodging index of a particular variety must include diameter of culm, root type and height of the plant, the relative importance of these characters being given numerically as 10 : 5 : 1.

Droogleever Fortuyn-van Leyden [11]) studied lodging phenomena in seven rice varieties. She concluded that in addition to a well-developed root system and strong longer internodes the development of a strong leaf sheath enveloping the internodes may be a valuable character in procuring standing ability. In some rice varieties with weak stems the strongly developed leaf sheaths enabled the plants to remain in an upright position until harvest time. This statement is in agreement with an earlier communication by Ramiah and Dharmalingam [29]). Furthermore these authors stress the importance of diameter of culm internodes and thickness of culm wall in securing lodging resistance in rice plants. Rivera [30]) ascribes the inadequate standing ability of plants supplied abundantly with nitrogen to the high water content of their culms.

With regard to the effect of mineral nutrition on lodging resistance there is agreement amongst various authors as far as the influence of nitrogen supply to the plants is concerned. Excessive amounts of available nitrogen in combination with favourable growing conditions often lead to the formation of a heavy crop possessing a high tendency to lodging. As far as the cause of this nitrogen effect is concerned, however, the opinions of various authors differ considerably. According to Kraus [21]), the great increase in weight of the higher parts of plants supplied with excessive nitrogen is often the cause of the increased liability to lodging. In addition the lower internodes may be weakened owing to reduced wall thickness and reduced thickening and lignification of the mechanical tissues of the culm. The latter is in agreement with the results obtained by Kissel [21]), Welton [38]) and Welton and Morris [39]). The former found a reduced cell wall thickness in oats and grasses treated with nitrogenous fertilisers. The effect was more pronounced in the parenchyma than in the sclerenchyma tissues and more so with nitrate than with ammonium nitrogen as the fertiliser. Welton found that oat plants grown on a fertile soil, rich in available nitrogen, had thinner culm walls and a less completely

lignified sclerenchymatous ring. In accordance with these structural differences the content of carbohydrates, including lignin, was found to be lower in the lodged plants. In contrast to these results, Phillips *et. al.* [27]) found a higher lignin content in the straw of lodged wheat plants dressed with sodium nitrate than in straw from non-lodged control plants which had not been fertilised with nitrogen. According to these authors a high lignin content makes the stems less resistant to lodging.

Purvis [28]) investigated the effect of potassium deficiency on the standing ability and the anatomy of the stem of *Dactylis glomerata*. The strengthening effect of potassium was found to be very pronounced. Frequently the grass on plots without a K-dressing was completely flattened, whereas that on the neighbouring plots supplied with potassium was still standing. In contrast to the strengthening of the plants, the thickening of the sclerenchyma cell walls in the stems was not favoured by an improved K-nutrition. The sclerenchyma walls were thinner where potassium had been supplied especially during the early stages. Apparently the rigidity of the plants well-supplied with potassium was not the result of anatomical strengthening. Tubbs [35]) found potassium-deficient barley plants to have much weaker lower internodes than plants which had been fully manured. P-deficient plants and particularly those with nitrogen deficiency had the strongest lower internodes. This was concluded from measurements of the force required to crush 1 cm length of straw. In agreement with these measurements the culm wall thickness of the lower internodes of potassium-deficient plants was found to be much less than that of fully manured plants. The thickness of the sclerenchymatous ring of K-starved plants was practically unchanged in comparison with normal plants but a striking reduction of lignified parenchyma was found in the former plants. Krantz and Chandler [23]) found that potassium dressings decreased lodging in corn (maize) only in those cases where visual symptoms of K-deficiency occurred in the undressed plants.

Kissel [21]) observed a thickening effect of phosphate dressings on cell walls in oats and in two grasses.

The lodging of cereals due to fungal attack (*Cercosporella herpotrichoiaes*) was not considered in the present investigations. When the density of the crop is not too great, nitrogen dressings may enable the plants to partly overcome the detrimental effect brought about by this fungus (Bockmann [4])). Care was taken to ensure that the crops in which lodging phenomena were studied were free from *Cercosporella* attack.

2. EXPERIMENTAL METHODS

Experiments were laid out on various soils in the northern part of the Netherlands. The cereals were sown at the rate of approximately 100 kg per ha in the case of oats and barley and 150 kg per ha in the case of rye and wheat. The spacing was generally 20 cm; in

some experiments various spacings have been used. Nitrogen was applied in different amounts, usually in the form of ammonium nitrate limestone. In those cases in which no interactions between nitrogen and other nutrient elements were to be studied, the whole area was amply dressed with phosphate, potassium and in some instances with magnesium and copper. Where the effect of phosphorus, potassium and other elements in relation to nitrogen nutrition on lodging were to be studied, the experiments were laid out on soils poor in these elements.

Degree of lodging has been recorded as a lodging index ranging from 0–10. These indices were obtained by multiplying area of lodged crop by degree of lodging (0 = erect, 10 = total area completely flattened).

In order to determine the effect of excessive amounts of nitrogenous fertilisers on various plant characters, independent of lodging, part of the crop on some plots was supported by ropes so that the plants were forced to keep their upright position (see Plate 1).

In some cases use was made of pot experiments for studying the effect of different fertiliser treatments in combination with different degrees of illumination.

For the measurement of various plant characters in relation to tendency to lodging samples of from 50 to 100 culms per plot were collected at different stages between flowering and ripening. For this purpose the plants were dug out of the soil in such a way that the upper parts of the roots remained attached to the base of the culm. No attempt was made, however, to collect the whole root system. The samples were used for measuring a number of plant characters such as length and diameter of internodes, weight per unit length of culm, and thickness of culm wall, thickness and lignification of sclerenchymatous ring, wall thickness of sclerenchymatous cells and number of vascular bundles. The latter characters were measured microscopically in hand-prepared cross sections cut from the middle portions of the second lowest internodes. To weaken the lignified tissues the straws were boiled in water for 15 minutes. They were stained by phloroglucinol and hydrochloric acid.

In those cases in which the relation between lodging and root development were to be studied, a method employed by Dr M. A. J. Goedewaagen [14, 15], of this station was followed. A pit was dug approximately one meter deep and half a meter wide. A board 90

by 30 cm and studded with pins 8 cm long and 5 cm apart, was then pushed into the vertical wall of the pit. The soil was cut 1 cm beyond the end of the pins after which the slab of soil containing the roots of approximately ten cereal plants was carefully dug out and removed to the laboratory. Because of the pins the soil could be washed away without altering the natural structure of the root system.

Analytical methods

Lignin was determined according to a modified method of Klason (cf Brauns[7]). 1 g of ground straw was weighed into a flask of 1 l capacity. To this 20 cc of 80 percent sulphuric acid was added and the mixture was allowed to stand at 20° C for 30 minutes with occasional stirring. The mixture was then diluted with water to 500 cc and boiled gently for a further 30 minutes to complete hydrolysis of carbohydrates. The residue was filtered on a weighed filter in a Büchner funnel, washed free of acid with 1 l hot water, treated once with acetone, dried, weighed and ashed. A second sample treated in a similar way was used for determining nitrogen. Lignin was calculated on an ash-free and protein-free basis. In some cases the ground material was refluxed for 8 hours with a mixture of two parts ethanol and one part benzene, followed by an extraction with water of 60° C during 24 hours (cf Goss and Phillips[17]).

3. PLANT CHARACTERS RELATED TO TENDENCY TO LODGING

Lodging of cereals often results from the combined effects of an inadequate standing power of the crop and adverse weather conditions prevailing during some part of the period from ear emergence to ripening. When growing conditions during the period of stem elongation have been favourable for the development of plants with a great tendency to lodging, these plants may remain erect if, during the subsequent two months, there is no heavy rain and wind. On the other hand plants relatively resistant to lodging may fall down when exceptionally bad weather prevails from flowering to ripening.

From these considerations it will be seen that tendency to lodging is not identical with lodging itself. Since the grower can influence the liability of a crop to lodging but not the weather conditions, it is clear that investigations concerning the effect of various conditions on lodging have to consider tendency to lodging rather than lodging itself. This applies particularly to those regions where rainy weather does not prevail regularly between ear emergence and ripening of the cereals. In the Netherlands as in other regions with a marine

climate where such weather is very common during July and August, tendency to lodging will often result in the cereal crop falling down. There are exceptions, however, and the author has therefore investigated the effect of a number of nutritional conditions on lodging itself as well as on a number of plant characters closely related to tendency to lodging. Before discussing the relative value of these plant characters as a measure for tendency to lodging, a short description will be given of the structure of the culm of cereals *).

Generally the culm of cereals is a hollow cylinder consisting of from 5 to 7 internodes. The length of these internodes is smallest at the base of the culm; it increases considerably towards the top. Although from the point of view of resistance to bending it is most desirable that the lower internodes have the greatest diameter, very often this is not the case. The highest and the lowest internodes have generally the smallest diameter. The wall thickness and the degree of lignification, however, have their greatest development in the lower parts of the stem.

The leaf sheaths which surround a considerable part of the internodes presumably play an important role in strengthening the stem particularly when the tissues are still green and weak. This does not apply to the lower internodes, the sheaths of which wither at an early stage.

Anatomically the culm internodes consist of the following tissues:

a) The epidermis.

b) A zone of sclerenchymatic tissue beneath the epidermis, called "hypoderm" by some authors [26]). The lignified fibres have narrow lumina and strong walls. The number of lignified cells as well as the wall thickness is variable.

c) Embedded in the sclerenchymatous ring are bands of green assimilating parenchyma which run parallel along the stem.

d) Large-celled ground parenchyma extending from the sclerenchymatous ring to the central cavity. The walls of these parenchyma cells are sometimes lignified.

e) Vascular bundles. There exist two types of vascular bundles, viz. small ones which are situated in a ring in the sclerenchymatous tissue whilst nearer to the centre in the parenchyma large bundles are found, arranged more or less regularly in a ring.

As has been stated earlier, lodging may occur as a result of irreversible bending or breaking of the lower internodes or of uprooting *i.e.* bending or breaking of the roots. Although the author has observed in some cases, particularly following heavy rain storms, that lodging of cereals was due to uprooting without any bending of the stems,

*) For a more detailed description of the culm of wheat plants see Percival [26]).

in by far the majority of cases irreversible bending of the stem at its lower internodes was found to be associated with the lodging of the crop. Sometimes a combination of bending of the lower internodes and of bending and breaking of the roots may be found to occur in lodged cereals (see also K r a u s [24])).

From these considerations it may be seen that the tendency of a crop to lodging depends on one or more of the following three characteristics:

a. Resistance of the culms to bending. This applies particularly to the lower internodes which have to resist the greatest moment of force.

b. The development of the root system and its anchorage in the soil. A culm highly resistant to bending may be useless in preventing lodging if its roots are weakly developed.

c. Weight of the higher internodes of the stems plus leaves and heads in relation to the length of the culms. The heavier the higher parts of the stem and the greater the distance from their centre of gravity to the base of the culm the greater the moment of the forces acting upon the lower internodes and the roots.

a. *Resistance of the culm to bending*

The resistance to bending of a culm internode depends to a large extent on its diameter and wall thickness. Since the diameter of the lower internodes is often correlated negatively with its length, the latter characteristic likewise has been studied in relation to liability to lodging. It should be stressed, however, that the length of the lower internodes as such has no effect on its resistance to bending.

Further characteristics of the culm which may be considered to be highly important in connection with tendency to lodging are the structure and chemical composition of the culm wall. The occurrence of a sclerenchymatous ring in the outer layer of the stem undoubtedly contributes materially to the strength of the culm. Since the number of lignified cells as well as the wall thickness of these cells varies considerably under the influence of external conditions, much attention should be paid to these characters in relation to tendency to lodging. The number of vascular bundles and their structural composition as well as the lignification of the ground parenchyma also may be related to the strength of the culm.

b. *Root development and tendency to lodging*

Lodging-resistant crops should have, in addition to sturdy lower stems, a large proportion of strongly developed coronal roots which extend more or less horizontally through the soil. Roots with a greater tendency to grow downward in the soil are of less importance in this respect [8] [19].

c. *Weight of higher internodes, leaves and head*

Whether the tendency to lodging is due to an inadequate resistance of the lower internodes to bending or to a poorly developed or poorly anchored root system, in both cases it will be affected adversely by a heavy weight of the upper parts of the plant. This weight may be considerably increased by adhering rain water. Welton and Morris [39] found that in oat plants this may amount to approximately one-fifth of their own green weight.

4. EFFECT OF NITROGEN NUTRITION ON LODGING AND ON PLANT CHARACTERS RELATED TO TENDENCY TO LODGING

a. *Nitrogen nutrition and lodging*

The effect of nitrogen nutrition on the lodging of cereals has been investigated in a number of field experiments laid out on different soils during the years 1940 to 1949. A considerable increase in lodging was observed in most cases when the nitrogen nutrition of the plants had been more excessive (Fig. 1). This is in agreement with practical experience and with the results of many experiments described in the literature.

On different soils and in different years, however, the results were not identical. This was partly due to differences in soil fertility, particularly in available soil nitrogen and moisture supply, and partly to differences in climatic conditions. Soils rich in available nitrogen require less fertiliser nitrogen to produce a heavy crop with a great tendency to lodging than do poor soils. In addition to the nitrogen supply of the crop, favourable climatic conditions during the period of elongation of the basal culm internodes of the cereals are required for the production of plants with a great liability to lodging. If during this period the weather is very dry or cold the rate of growth of the plants is reduced as a result of which tendency to lodging is low while lodging itself even at excessive nitrogen levels

does not usually occur. Such conditions, which may be common in regions with a dry climate, are relatively exceptional in the Netherlands. They may be found more frequently on high sandy

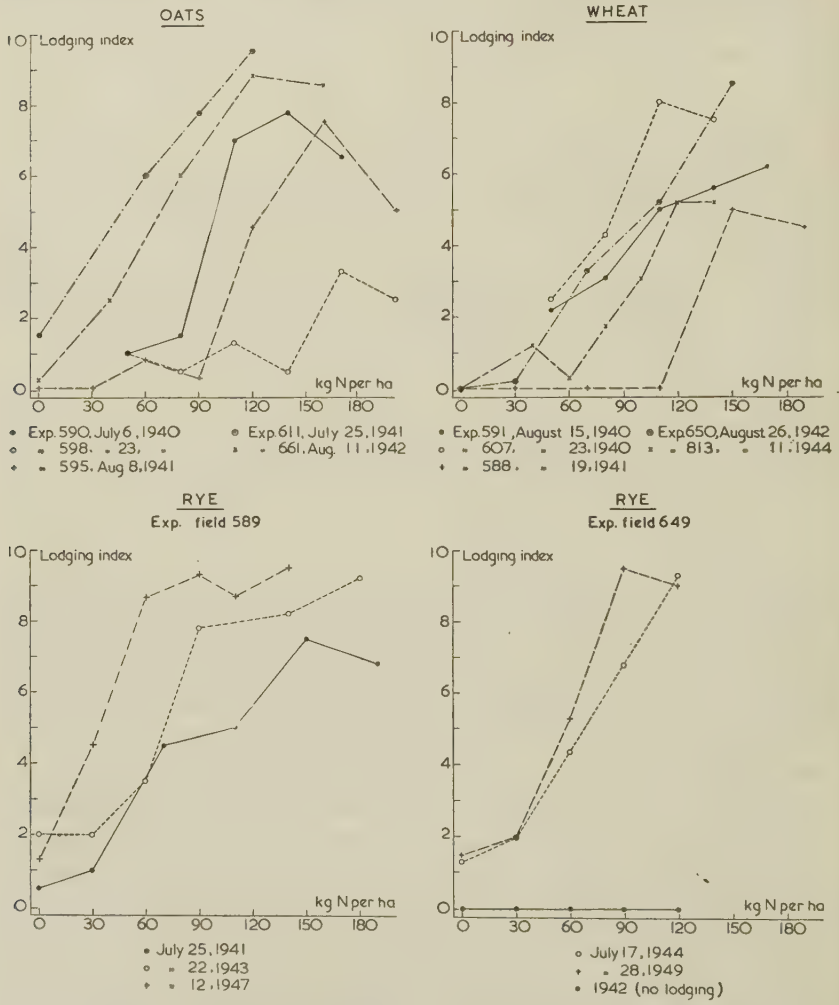


Fig. 1. Effect of nitrogen dressings on lodging of oats, summer wheat and winter rye. 0 = erect, 10 = completely flattened.

soils with a poor water-holding capacity than on peaty and clay soils. The oats on Experimental plot 598 suffered from such a drought period in 1940 and practically no lodging occurred even at a

dressing of 200 kg N per ha (Fig. 1). On Exp. plot 590, however, where the plants did not suffer from shortage of water in 1940, the crop was almost completely lodged when 110 kg of nitrogen per ha or more had been applied.

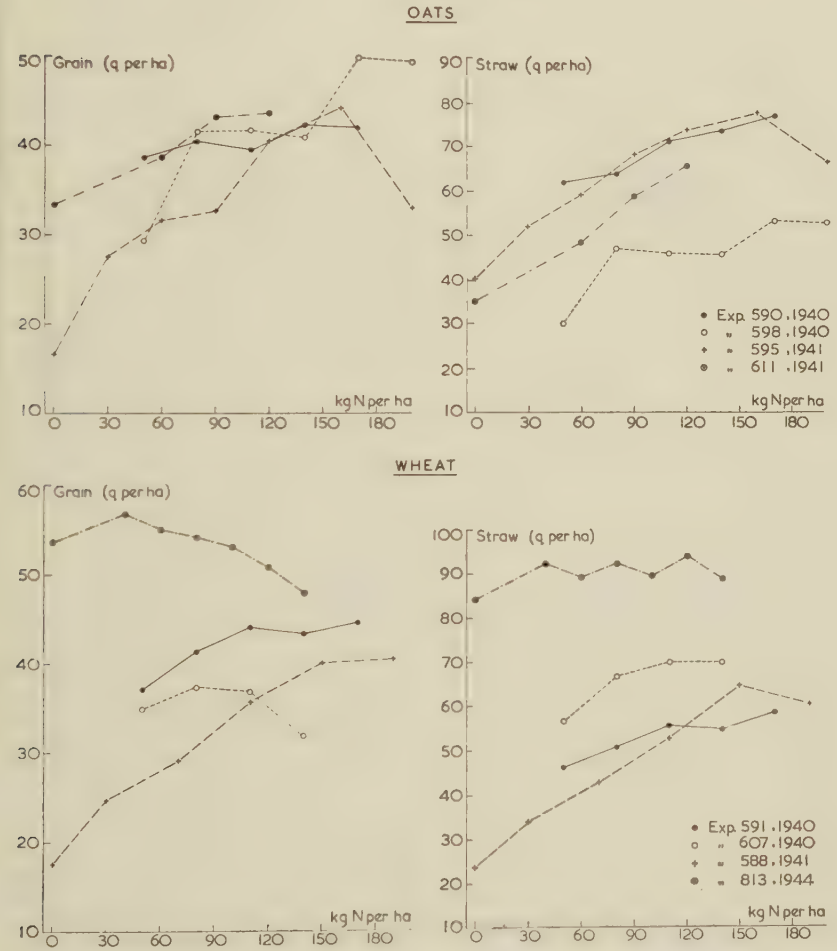


Fig. 2. Effect of nitrogen dressings on yield of oats and wheat (1q = 100 kg).

When the drought period is of a short duration, as was the case with Exp. 598, grain production may not be reduced appreciably. Straw production on this plot, however, was much lower than that on Plot 590, where the grain production suffered seriously from

lodging (Fig. 2). When the drought period persists for a longer period of time, however, the grain yield will be considerably lower.

The important effect of climatic conditions on lodging may be

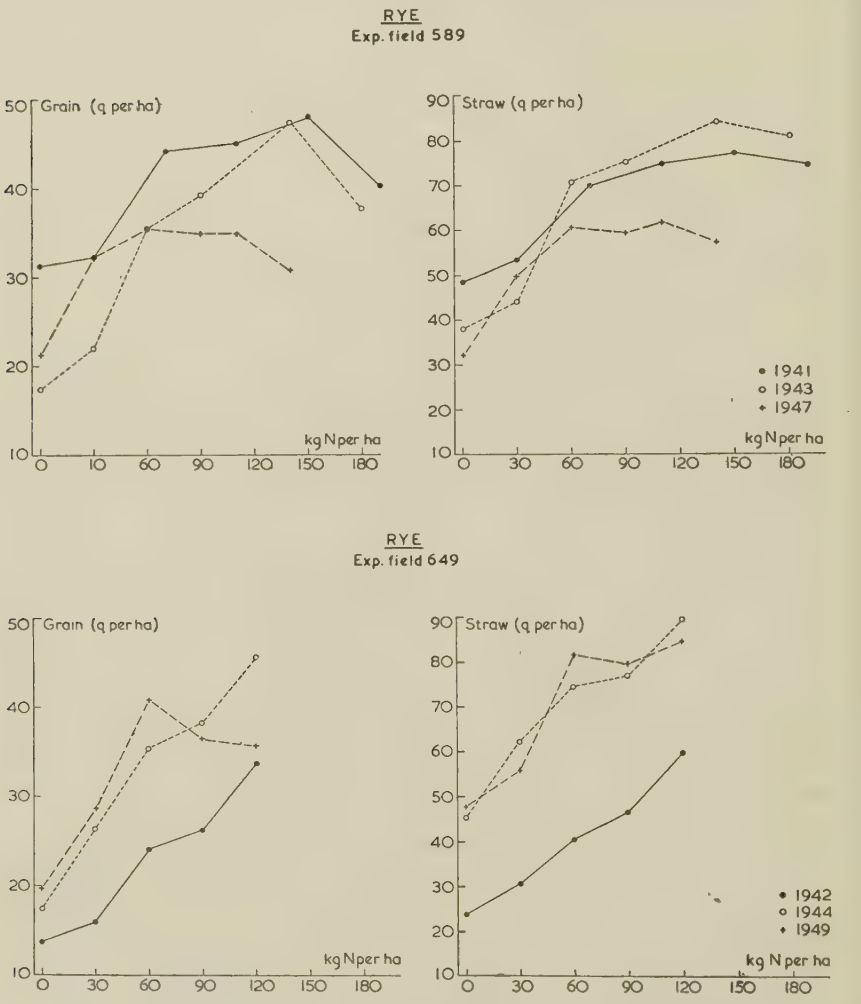


Fig. 3. Effect of nitrogen dressings on yield of rye (1q = 100 kg).

seen particularly from those experiments in which the same cereal was cultivated on the same area in different years (Experiments 589 and 649 in Fig. 1). The large differences in lodging of rye observed on these plots may have been due to differences in weather

Fig. 4. Average daily temperature and average daily precipitation per 10 days in different years.

conditions during the growing period of the crops resulting in plants with a widely varying liability to lodging. They may also have been caused, however, by differences in weather conditions between blooming and ripening. Heavy rain storms during this period may beat down crops which under more favourable weather conditions would have remained erect.

On Plot 649 the absence of lodging in 1942 was apparently a result of the very dry spring, with no rain between April 10 and May 10 (cf Fig. 4). As a result the crop responded inadequately to the nitrogen dressings which had been applied on April 17. The rain storms which occurred rather frequently in 1942 were unable to bring about lodging of the crop.

In the case of Plot 589 the severe lodging of the crop in 1947 apparently resulted from both a relatively high tendency to lodging due to favourable growing conditions in the spring and a heavy thunderstorm on June 5.

A further factor which may be responsible for the differences in lodging in different years is the amount of available soil nitrogen which may vary under the influence of temperature and rainfall in the preceeding months. From the course of the yield curves in Fig. 3 it could be concluded that the rye of Plot 649 in 1942 was supplied less abundantly with soil nitrogen than in 1944 and 1949.

b. *Effect of nitrogen nutrition on plant characters related to tendency to lodging*

1. Length of internodes. One of the plant characters which have been studied extensively in relation to lodging is the length of the various internodes of the culm. It is a well-known fact that etiolated plants form long, slender and weak stems. Since nitrogen nutrition promotes the stooling of cereal plants and the formation of leaf material, it will bring about a considerable shading of the lower parts of the stem.

For the measurements of the internodes samples of from 50 to 100 culms from plots dressed with different amounts of fertiliser nitrogen were collected at various times between flowering and ripening. In some cases samples have been taken from lodged and non-lodged areas of the same plot or from general fields. The results of these determinations are given in Table 1 and in Fig. 5. Since the number of internodes of the various culms of the samples varied

from five to seven, or sometimes eight, average values have been calculated of culms with equal numbers of internodes.

It should be stressed that the length of the internodes has been

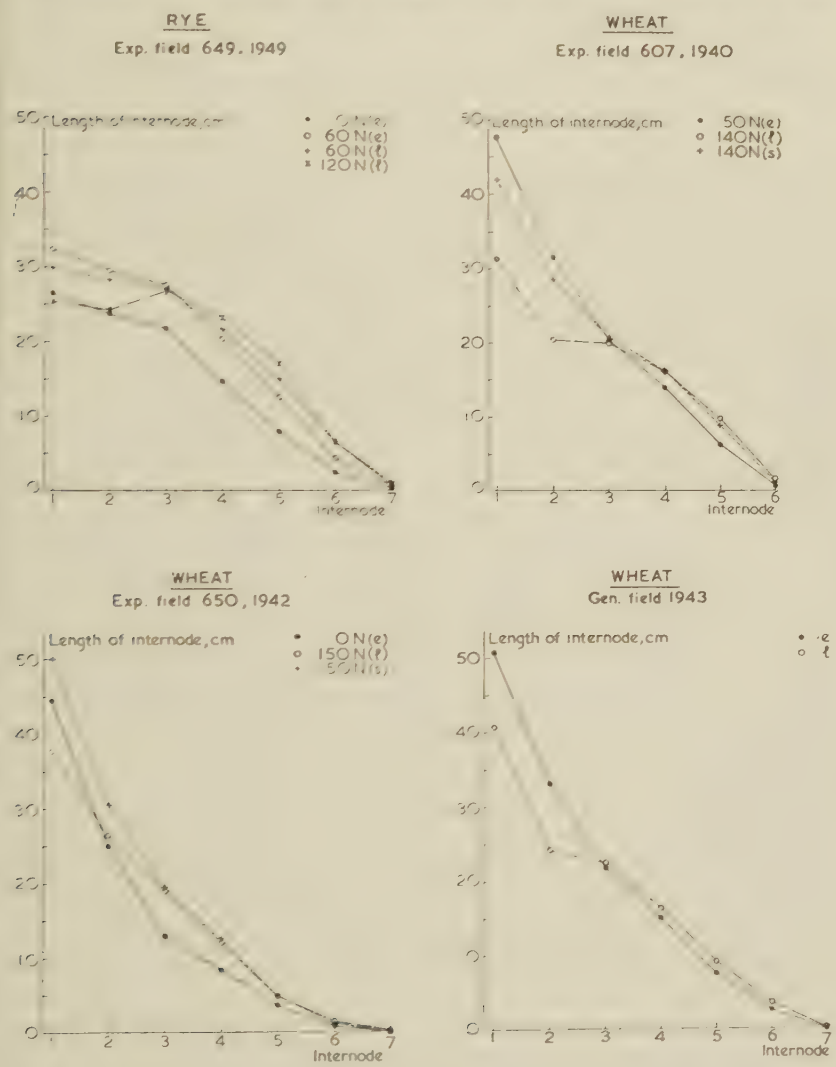


Fig. 5. Length of internodes of cereal culms at different nitrogen dressings. e = erect, l = lodged, s = supported plants, 1st = highest internode.

ascertained with the naked eye, so that values which could not be easily measured in this way, viz. those shorter than 2–3 mm were

TABLE I

Effect of nitrogen nutrition of cereal plants on length of internodes *)

Cereal, **) experiment, year and soil	Kg N per ha	Lodged (l) or erect(e)	Number of culms per sample***)	Number of internodes per culm	Average length of internodes, cm								Total length of culm, cm
					1st	2nd	3rd	4th	5th	6th	7th	8th	
Winter rye, 589, 1947, sandy	0	e	5	5	41.4±1.2	33.2±1.4	21.1±1.1	6.0±1.6	1.6±0.3	—	—	—	103.3± 1.9
			69	6	38.4±0.7	30.6±0.6	19.8±0.3	10.7±0.3	3.9±0.3	0.8±0.1	—	—	104.2± 1.6
			54	7	36.1±0.7	28.6±0.5	20.3±0.4	13.0±0.3	5.9±0.3	1.6±0.1	0.6±0.1	—	106.1± 1.6
	30	e	8	5	44.9±2.2	37.0±1.6	20.8±1.0	10.1±1.4	1.9±0.4	—	—	—	114.7± 3.1
			90	6	43.1±0.7	35.9±0.6	22.1±0.3	12.8±0.3	4.3±0.3	0.8±0.1	—	—	119.0± 1.2
			93	7	43.0±0.6	35.5±0.5	23.0±0.3	14.7±0.3	6.8±0.3	1.6±0.1	0.7±0.0	—	125.2± 1.2
	60	e	33	5	46.7±1.0	35.6±0.7	17.8±0.6	8.5±0.6	1.2±0.2	—	—	—	109.8± 1.5
			87	6	42.6±0.4	34.1±0.5	19.4±0.3	11.7±0.3	4.3±0.3	0.7±0.1	—	—	112.8± 1.0
			56	7	41.4±0.9	33.6±0.5	21.5±0.4	13.8±0.4	6.7±0.4	1.5±0.2	0.4±0.0	—	118.9± 1.4
	140	l	21	5	43.1±1.5	34.7±1.5	22.5±0.6	9.8±1.3	1.6±0.4	—	—	—	111.7± 2.4
			145	6	39.2±0.6	30.3±0.5	24.0±0.3	16.8±0.4	6.1±0.4	1.1±0.1	—	—	117.5± 0.9
			109	7	38.5±0.6	30.1±0.6	24.6±0.3	18.5±0.4	9.2±0.5	2.0±0.2	0.5±0.0	—	123.4± 1.0
Winter rye, 649, 1949, peaty	0	e	4	5	29.0±0.6	26.2±1.1	20.7±0.4	10.1±0.8	3.9±0.4	—	—	—	89.9± 2.5
			66	6	27.0±0.7	25.2±0.6	21.5±0.4	13.7±0.3	7.2±0.2	1.5±0.1	—	—	96.1± 1.8
			34	7	25.2±0.7	22.2±0.7	22.4±0.5	16.0±0.4	9.7±0.4	4.6±0.3	0.5±0.1	—	100.6± 1.9
	60	e	3	5	34.2±1.8	36.6±1.6	28.6±2.4	17.1±1.3	4.9±0.3	—	—	—	121.4± 6.6
			37	6	30.3±1.2	29.2±1.0	27.5±0.5	20.3±0.5	12.3±0.5	3.1±0.3	—	—	122.7± 2.2
			16	7	31.2±1.6	29.1±1.7	28.4±0.7	20.3±0.9	14.3±0.8	6.2±0.9	1.0±0.2	—	130.5± 3.2
			2	8	28.3±4.3	25.8±6.8	23.8±2.1	18.4±0.9	13.9±0.2	8.8±1.3	2.7±1.0	0.5±0.2	122.2±14.4
	60	l	20	6	34.4±1.4	33.1±1.5	27.1±0.9	20.5±0.6	11.4±1.0	2.1±0.4	—	—	128.6± 3.1
			31	7	29.4±1.1	28.1±1.1	28.5±0.4	23.2±0.5	17.1±0.7	8.4±0.7	1.0±0.1	—	135.7± 1.6
			6	8	22.4±2.1	20.6±2.9	26.1±1.8	22.6±1.8	19.5±1.5	12.4±1.9	4.0±1.2	0.4±0.1	128.0± 7.1
	120	l	57	6	26.4±0.8	26.0±0.8	28.4±0.4	23.2±0.4	14.5±0.5	2.9±0.3	—	—	121.4± 1.7
			64	7	24.8±0.7	23.2±0.6	26.7±0.4	23.5±0.3	18.6±0.4	8.2±0.5	0.9±0.1	—	125.9± 1.4
			12	8	23.4±1.2	20.2±1.1	25.4±0.5	23.3±0.7	20.9±1.0	13.8±1.0	3.6±0.6	0.5±0.1	131.1± 1.7

*) The data for seven further experiments may be obtained from the author.
**) Culms of Exp. 589 collected two weeks before harvesting, those of Exp. 649 shortly after blooming.

omitted. Had a more accurate measurement been possible, the number of internodes in all culms of a particular crop would probably have been the same. Under certain circumstances the lower internodes may reach measurable lengths, in other cases they remain very short or even rudimentary. Since it is highly probable that culms of the latter type have very compact and sturdy basal parts, attention has been paid to the relationship between number of internodes and nitrogen nutrition.

The results of the measurements show that plants with an excessive nitrogen supply and which in general are very liable to lodge, have longer lower internodes than those grown on the same field with a low or moderate nitrogen supply (see also Fig. 5) *).

It is remarkable that the upper two internodes of plants well-supplied with nitrogen are frequently considerably shorter than those of plants dressed with moderate amounts. This is particularly true when lodging has occurred at an early date. When plants with a high liability to lodging had been supported by ropes so that they remained erect (Plate I) the upper internodes attained a normal length. This clearly shows the inhibiting effect of lodging on the growth of the upper internodes. The lower internodes of these supported plants, however, had approximately the same length as those of the lodged plants, indicating that the relatively long lower internodes of the latter plants was not a result of lodging.

The negative correlation between length of lower and higher internodes may likewise be found more or less clearly in unlodged plants. This will be seen when plants grown in a greenhouse are compared with those grown outdoors (cf Fig. 6). The former have longer lower internodes but shorter higher ones. It may also be concluded from the fact that plants with a larger number of measurable internodes have the shortest upper internodes (Table I). In the latter case it is assumed that an increase in the number of internodes simply means an elongation of the lowest so enabling them to be measured.

*) Since the number of measurable internodes is frequently higher when the nitrogen supply to the plants has been more abundant (see Table I), it will be clear that the differences in length of lower internodes between plants with varying nitrogen supply, will become more pronounced when average values for all plants in one sample have been calculated. In this case the assumption has been made that the number of internodes in all culms of a certain variety is constant. In Figs. 5 and 6 these average values have been plotted.

When a comparison is made between the lengths of the lower internodes of plants grown under various climatic conditions

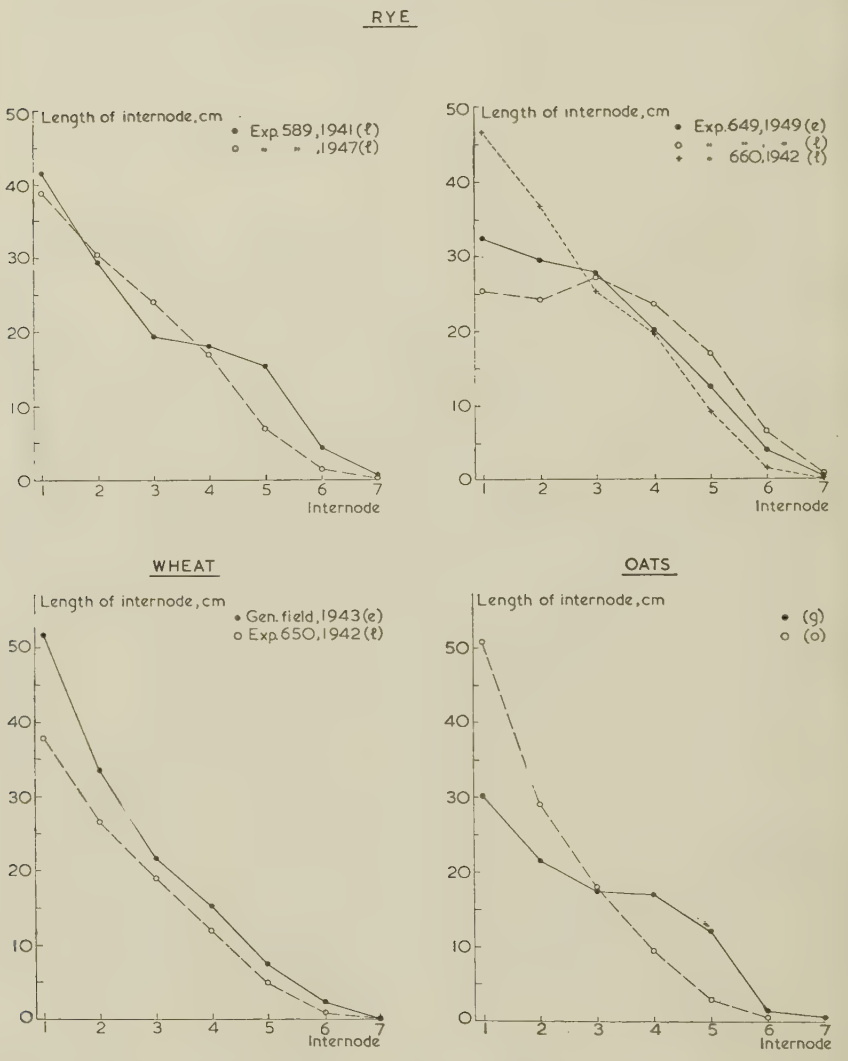


Fig. 6. Length of internodes of cereal culms at different nitrogen dressings. e = erect, l = lodged, g = grown in a greenhouse, o = grown in the field, 1st = highest internode.

(different years, greenhouse as compared with field conditions) it will be seen that the differences between these plants are sometimes

of much more importance than those found in plants of the same field grown at varying nitrogen levels. In the experiments with rye it was found that the length of the 5th and 6th internodes from plants grown in 1941 (Exp. 589) was more than twice the length of corresponding internodes from plants grown on the same field in 1947 (cf Fig. 6). In 1949 (Exp. 649) the length of the 6th internodes of lodged plants was four times the length of similar internodes in 1942 (Exp. 660). In the former year even the lowest internodes showed a considerable elongation. Since the spring of 1949 was characterized by exceptionally warm weather (cf Fig. 4) it is highly probable that the very rapid growth of the cereal plants which was further promoted by a favourable water and nitrogen supply in many fields has resulted in long, weak, lower internodes which had little resistance to bending. In this year lodging occurred in practically every rye field in the Netherlands.

Similar differences in the length of the lower internodes were found in the experiments with oats and wheat. Plants grown in a greenhouse had usually considerably longer lower internodes than those grown in the field (see Fig. 6). This is probably due to the higher temperature and somewhat reduced illumination under greenhouse conditions.

Although the long lower internodes of plants grown at high temperatures and with favourable water and nitrogen supplies are undoubtedly a valuable indication of the weakness of those plants, the data of Fig. 6, however, clearly show, that the length of these internodes cannot be used as a general index for liability to lodging. The lodged rye plants of Exp. 660 in 1942 for instance had considerably shorter lower internodes than the non-lodged plants of Exp. 649 in 1947. Similarly the erect wheat plants of the 1943 experiment had considerably longer lower internodes than the lodged plants of Exp. 650 in 1942. Apparently the long lower internodes of the erect plants had more resistance to bending than the relatively short ones of the lodged plants. Differences in root development and weight of heads and leaves may also have played a part in affecting the liability to lodging.

2. Number of internodes. Although it is not known whether plants with a greater number of internodes are more liable to lodging than those with a relatively small number, it is probable that the latter plants have more sturdy basal parts so that they

have a greater resistance to lodging than those with a higher number. From the results of Table I it can be seen that favourable growing conditions, particularly nitrogen supply, may promote the number of internodes measurable with the naked eye.

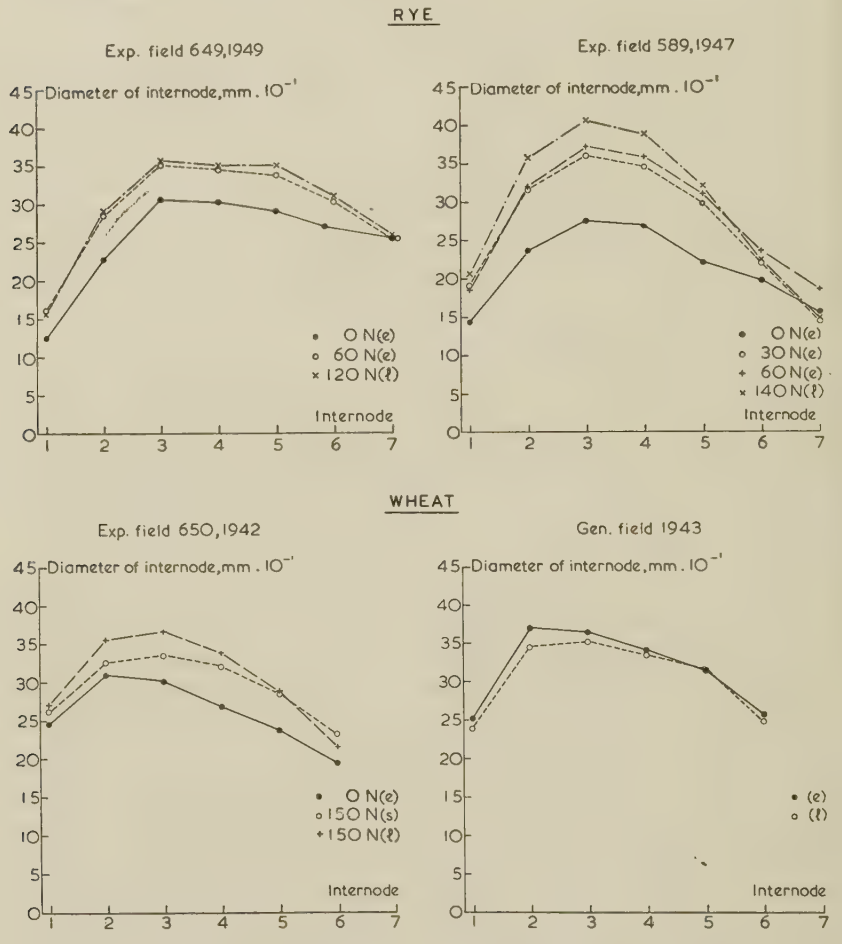


Fig. 7. Diameter of internodes of cereal culms at different nitrogen dressings. e = erect, l = lodged, s = supported plants, 1st = highest internode

3. Diameter of internodes. The culm diameter was measured at the middle of the internodes. The results of a number of measurements are given in Table II (see also Fig. 7). It will be seen that the 3rd or 4th internodes generally have the greatest

Effect of nitrogen nutrition of cereal plants on diameter of internodes *)

Cereal, experiment, year and soil	Kg N per ha	Lodged(l) or erect(e)	Number of culms per sample **)	Number of internodes per culm	Average diameter of internodes, mm.10^{-1}							
					1st	2nd	3rd	4th	5th	6th	7th	8th
Winter rye, 589, 1947, sandy	0	e	22	5	14.6 ± 0.7	23.8 ± 1.3	20.8 ± 1.1	25.5 ± 1.0	20.8 ± 0.9	—	—	—
			66	6	14.2 ± 0.4	23.1 ± 0.7	27.2 ± 0.8	26.2 ± 0.7	23.7 ± 0.7	18.2 ± 0.6	—	—
			49	7	15.1 ± 0.6	24.5 ± 0.8	28.2 ± 0.9	28.7 ± 0.9	26.0 ± 0.8	21.8 ± 0.7	15.5 ± 0.8	—
	30	e	50	5	19.7 ± 0.5	32.4 ± 0.8	36.3 ± 1.1	33.9 ± 0.9	27.9 ± 0.8	—	—	—
			92	6	19.2 ± 0.4	31.7 ± 0.6	35.9 ± 0.7	34.6 ± 0.6	29.8 ± 0.6	21.0 ± 0.6	—	—
			50	7	18.5 ± 0.6	30.9 ± 1.0	35.7 ± 1.1	34.4 ± 1.0	31.2 ± 0.9	24.3 ± 0.8	14.8 ± 0.7	—
	60	e	57	5	19.4 ± 0.4	33.0 ± 0.7	37.5 ± 0.8	35.3 ± 0.8	28.6 ± 0.7	—	—	—
			100	6	18.6 ± 0.4	31.5 ± 0.7	36.7 ± 0.7	35.8 ± 0.7	31.7 ± 0.6	23.2 ± 0.6	—	—
			24	7	17.9 ± 0.8	31.3 ± 1.4	37.4 ± 1.3	36.5 ± 1.2	32.8 ± 1.3	24.9 ± 1.3	18.5 ± 1.4	—
	140	l	70	5	21.6 ± 0.4	36.9 ± 1.2	40.9 ± 0.8	38.2 ± 0.9	29.3 ± 0.8	—	—	—
			152	6	20.3 ± 0.3	35.3 ± 0.5	40.1 ± 0.6	38.8 ± 0.6	32.6 ± 0.6	22.2 ± 0.6	—	—
			49	7	21.1 ± 0.5	35.8 ± 1.1	41.6 ± 1.0	39.1 ± 1.0	34.0 ± 1.0	24.2 ± 0.8	14.5 ± 0.6	—
Winter rye, 649, 1949, peaty	0	e	4	5	12.3 ± 0.9	21.5 ± 0.6	30.8 ± 2.5	26.0 ± 1.2	25.8 ± 1.3	—	—	—
			66	6	12.9 ± 0.5	24.0 ± 0.8	30.9 ± 0.8	30.9 ± 0.7	29.6 ± 0.7	26.5 ± 0.6	—	—
			34	7	11.7 ± 0.5	20.6 ± 0.8	29.6 ± 0.9	29.6 ± 0.9	28.6 ± 0.8	28.2 ± 0.9	25.4 ± 0.7	—
	60	e	3	5	19.7 ± 1.7	37.3 ± 0.4	39.3 ± 1.2	38.0 ± 1.5	36.7 ± 1.7	—	—	—
			37	6	15.1 ± 0.7	27.2 ± 1.0	34.4 ± 1.2	31.7 ± 0.9	32.7 ± 0.8	29.4 ± 0.9	—	—
			16	7	17.1 ± 0.3	29.4 ± 1.4	36.6 ± 1.2	35.4 ± 1.0	35.4 ± 0.9	33.3 ± 1.1	25.9 ± 1.1	—
			2	8	26.0 ± 7.0	34.5 ± 6.5	33.5 ± 5.5	35.5 ± 7.5	35.5 ± 7.5	29.5 ± 9.5	21.5 ± 6.6	—
	60	l	20	6	16.9 ± 0.7	30.5 ± 1.6	35.9 ± 1.7	32.7 ± 1.6	31.8 ± 1.3	28.5 ± 1.5	—	—
			31	7	15.3 ± 0.7	27.5 ± 1.2	35.4 ± 1.1	35.2 ± 1.1	34.6 ± 1.2	32.8 ± 1.1	26.1 ± 1.2	—
			6	8	12.6 ± 1.6	20.7 ± 2.4	30.2 ± 3.3	32.2 ± 2.7	31.3 ± 1.8	29.8 ± 2.7	26.0 ± 1.5	20.0 ± 1.0
	120	l	57	6	16.5 ± 0.6	29.6 ± 1.6	35.8 ± 0.6	35.4 ± 0.6	34.4 ± 0.7	29.2 ± 0.7	—	—
			64	7	14.8 ± 0.4	28.8 ± 0.8	35.4 ± 0.7	35.3 ± 0.7	35.3 ± 0.7	31.8 ± 0.7	24.8 ± 0.7	—
			12	8	14.5 ± 0.8	26.7 ± 1.8	36.7 ± 1.6	36.0 ± 1.5	36.8 ± 1.5	34.1 ± 1.4	30.5 ± 1.2	22.9 ± 1.0

*) The data for seven further experiments may be obtained from the author.

**) Classified according to number of internodes. In Experiment 589 classification for measurements of length and diameter have been carried out at different dates.

diameter. Plants supplied with inadequate amounts of nitrogen have smaller culm diameters than those with a normal nitrogen supply. With excessive amounts of nitrogen the diameter of the higher internodes may sometimes be increased; the lower internodes, however, have equal or smaller diameters.

When culms with different numbers of measurable internodes in the same samples are compared it appears that as the number of internodes increases the diameter of the lowest ones decreases. This means that increase in internode numbers which may be brought about by excessive nitrogen dressings may reduce the resistance to bending of the culm base.

4. Culm wall thickness. Culm wall thickness like culm diameter is an important property in providing resistance to bending and breaking of cereal culms. The thickness of the culm wall was measured microscopically in the same sections which were used for the measurement of anatomical features. These sections were cut from the middle portions of the second lowest internodes. The results of these measurements are given in Table III. It will be seen that lodged plants which have been supplied excessively with nitrogen may have thinner culm walls than erect plants grown on the same soil at a lower rate of fertiliser dressing. This was the case with the oat plants of Exp. 661, the wheat of Exp. 650 and the wheat of the farmer's field. In the case of the rye plants of Exp. 649 no effect of nitrogen nutrition on culm wall thickness was observed while those of Exp. 589 even had the greatest wall thickness at the highest nitrogen dressing.

In those cases in which culms with different numbers of measurable internodes in the same sample had been investigated, it appeared that those with a greater number of internodes generally had a greater culm wall thickness in the lowest internodes. This means that the decrease in resistance to bending of these plants as a result of decreased culm diameter of the lowest internodes was presumably counterbalanced by an increase in culm wall thickness of these internodes.

5. Thickness of sclerenchymatous ring. The thickness of the sclerenchyma zone of the culm was measured at two quite different places in the transverse section of the second lowest internodes viz. a) where vascular bundles were absent and b) where a small vascular bundle was situated inside the sclerenchyma. In the

TABLE III

of nitrogen nutrition of cereal plants on culm wall thickness and anatomical characteristics of the second lowest culm internodes

xp., soil	Kg N per ha	Lodged (l) or erect (e)	Number of culms used **)	Number of internodes per culm	Culm wall thickness, μ	Thickness of sclerenchymatous ring, μ		Lignified tissue as % of total area of scl. ring	Thickness of sclerenchyma cell walls, μ	Number of vascular bundles
						A ***)	B ***)			
ye,	0	e	14—16	6	543±21	85±14	121±16	76±4	3.5±0.17	24±0.8
49,			9—10	7	593±41	84±9	135±20	68±4	3.6±0.25	26±0.8
	60	e	18	6	509±25	81±4	121±7	79±3	3.4±0.15	27±0.9
	60	l	8	6	587±27	76±4	115±3	64±7	3.5±0.22	26±1.6
			4	7	635±61	78±12	116±10	55±3	3.5±0.17	30±1.2
	120	l	26—30	6	578±17	82±5	124±4	65±3	2.4±0.10	27±0.8
ye,	30	e	59—60	—	570±17	73±2	—	—	3.9±0.11	—
47,	60	e	60	—	567±15	71±2	—	—	4.1±0.11	—
	140	l	59—70	—	726±17	64±1	—	—	2.5±0.10	—
,Gf*),	80	e	21—30	6	1009±27	96±2	130±3	82±3	5.7±0.11	31±0.5
eaty	80	l	27—30	6	876±19	71±2	108±2	71±3	4.3±0.03	30±0.8
1,	0	e	20—24	5	736±45	71±4	117±6	84±2	6.4±0.20	23±1.0
eaty			3—6	6	933±86	92±16	150±11	75±8	7.3±0.26	22±1.6
	160	l	25—29	5	566±16	70±2	110±2	84±2	5.3±0.15	22±0.4
			27—33	6	672±23	96±4	134±3	69±2	6.3±0.14	22±0.5
t,	0	e	25—28	5	703±22	84±3	116±3	99±0	5.9±0.10	25±0.2
42,			9—11	6	816±45	96±6	140±6	88±5	5.7±0.18	25±1.0
	150	l	22—24	5	649±24	81±3	125±4	93±2	4.6±0.15	26±0.5
			44—48	6	724±20	90±3	130±3	81±2	5.2±0.13	26±0.3

= general field.

ns collected: Exp. 649 shortly after blooming, Exp. 589 two weeks, Gf and Exp. 661 a few days and p. 650 four weeks before harvesting.

no vascular bundle, B: vascular bundle inside sclerenchymatous ring.

latter case the sclerenchyma zone always is considerably thicker.

As may be seen from Table III the thickness of the sclerenchymatous ring was unaffected by the nitrogen nutrition in the case of the rye of Exp. 649 and the wheat of Exp. 650. In the oats of Exp. 661 nitrogen manuring tended to reduce the development of the sclerenchyma. In the rye of Exp. 589 and the wheat of the general field the thickness of the sclerenchyma zone of the lodged plants was considerably reduced. Since a strong sclerenchymatous ring is of much importance for the standing ability of the culm, a reduction

of this tissue undoubtedly enhances the liability of the plant to lodging.

6. Thickness of sclerenchyma cell walls. Of all the anatomical characters studied thickness of sclerenchyma cell walls was affected most consistently by nitrogen manuring. In the lodged rye plants of Exp. 589 and Exp. 649 the greatest reduction in lignification was found (Table III and Plate II A and B).

7. Thickness of lignified parenchyma cell walls. In addition to thickness of sclerenchyma cell walls, lignification of the exterior layers of inner parenchyma was found to be clearly reduced in the case of ample nitrogen supply. Although no measurements of this character have been carried out, the microphotographs clearly show the differences in wall thickness of these parenchyma cells (Plate II A and B).

8. Area of lignified tissue in sclerenchymatous ring. As was described in section 3, bands of green parenchyma are embedded in the sclerenchyma. The extension of these bands appeared to be affected by the nitrogen nutrition of the plants. Lodged plants, supplied excessively with nitrogen often have larger parenchyma bands than those supplied poorly with nitrogen. This may be concluded from Table III, column 9, where a large area of lignified tissue corresponds with a poor development of the parenchyma bands.

9. Lignin content of basal culm internodes. The results of a number of lignin determinations in the second lowest internodes of cereal culms are recorded in Table IV. It will be seen that in general the lodged plants have a lower lignin content in their basal culm internodes than the non-lodged plants. The differences are less pronounced, however, than in the case of thickness of sclerenchyma cell walls.

10. Number of vascular bundles. According to Moldenhawer[25]) wheat varieties resistant to lodging have a greater number of vascular bundles than those with a great tendency to lodging. This statement was denied by Caffrey and Carroll[8]) but Hamilton[19]) found a larger number of vascular bundles in a lodging-resistant oat variety than in a non resistant one.

In the present study it was observed that oat culms have a smaller number of vascular bundles than rye and wheat culms. The latter apparently possess the greatest number. No effect of nitrogen nutri-

TABLE IV

Effect of nitrogen nutrition of cereal plants on lignin content of the lower culm (second lowest internodes)

Cereal *)	Experiment, year and soil	Kg N per ha	Lodged (l) or erect(e)	Lignin, % of dry matter
Winter rye	589,	0	e	19.3±0,07
	1947,	30	e	19.3±0.28
	sandy	60	e	19.5±0.08
		140	l	16.0±0.12
Winter rye	649,	0	e	15.1±0.26
	1949,	60	e	17.7±0.04
	peaty	60	l	16.9±0.13
		120	l	16.9±0.09
Summer wheat	General field	80	e	20.3±0.35
	1943, peaty			19.1±0.24 **)
		80	l	18.5±0.24
				17.4±0.37 **)
Summer wheat	650,	0	e	19.7±0.03
	1942,			15.7±0.17 ***)
	peaty	150	l	17.6±0.12
				14.3±0.43 ***)
Oats	661,	0	e	21.3±0.10
	1942,			18.6±0.11 **)
	peaty	160	l	20.5±0.04
				18.2±0.21 **)

*) Culms collected: Exp. 589 two weeks before harvesting, Exp. 649 shortly after flowering, Gf and Exp. 661 a few days and Exp. 650 four weeks before harvesting.

**) Sample pre-treated with ethanol-benzene mixture, followed by an extraction with water at 60° C.

***) Third lowest internodes.

tion was found as may be seen in Table III column 11. The degree of lignification of the vascular bundles, however, is clearly affected by the nitrogen nutrition. In agreement with the lignification of the sclerenchymatous ring which is reduced by an ample nitrogen supply, it was found that the layer of lignified cells surrounding the vascular bundle was clearly more lignified when the nitrogen nutrition of the plants had been inadequate.

11. Weight per cm of culm length in lower internodes. Weight per unit length of culm base was found by Atkins[2]) to be positively correlated with breaking strength of the straw. It is obvious, however, that ahigh value for this

character is of much importance in the standing ability of the plant only if the dry matter available is distributed in such a way that a high resistance to bending and breaking has been attained.

The weight of an internode per unit of length depends on a) cnlm diameter, b) thickness of culm wall and c) chemical composition of the culm wall.

TABLE V

Effect of nitrogen nutrition of cereal plants on weight per cm of culm length (second lowest internodes)

Cereal	Exp. and year	Kg N per ha	Lodged(l) or erect(e)	Weight per cm of culm length, mg			
				5 ††)	6	7	8
Winter rye	649, 1949	0	e	—	16.3±1.6	17.4±2.3	—
		60	e	—	15.9±1.4	—	—
		60	l	—	17.4±1.8	16.4±0.8	—
		120	l	—	13.3±0.8	14.6±0.7	15.6±1.0
Winter rye	660, 1942	0	e	—	16.2±0.6	16.5±1.0	—
		160	l	—	16.3±1.7	—	—
		160	s †)	—	15.7±0.9	16.0±1.6	—
		160	s	—	12.7±0.7	12.3±1.2	—
Summer wheat	650, 1942	0 *)	e	14.2±0.8	15.1±1.0	—	—
		150 *)	l	12.8±1.3	14.2±1.1	—	—
		150 *)	s	12.5±0.6	12.9±0.8	—	—
		0 **)	e	12.6±0.5	15.7±1.5	—	—
		150 **)	l	—	14.1±0.6	11.8±0.3	—
		150 **)	l	15.6±1.6	16.1±0.7	—	—
		150 **)	s	12.0±0.7	12.7±1.3	14.4±1.1	—
Summer wheat	General field, '43	80	e	—	—	19.2±0.4	—
		80	l	—	—	15.6±0.3	—
Oats	661, 1942	0	e	16.6±0.8	19.6±1.0	—	—
		80	e	17.9±1.3	18.9±1.0	—	—
		160	l	13.5±0.6	14.8±0.5	—	—
		160	s	12.7±0.7	13.8±1.9	—	—

*) 100 kg K_2O per ha. **) 300 kg K_2O per ha.

†) s = supported.

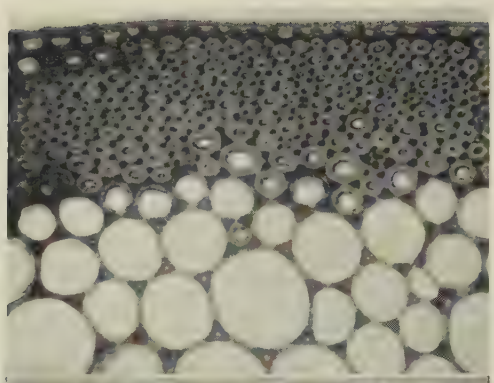
††) Culms with 5, 6, 7 and 8 internodes respectively.

As will be seen from the results in Table V the highest values for this property have generally been found in plants dressed with a low or moderate amount of fertiliser nitrogen. With an ample nitrogen supply considerably lower weights have been found.

12. Root system. Preliminary observations on the root system of lodged and erect plants showed that in general the latter had more

Plate I. Lodged oat and wheat plants amply dressed with nitrogen. Part of the plots supported by ropes to prevent lodging.

A



B

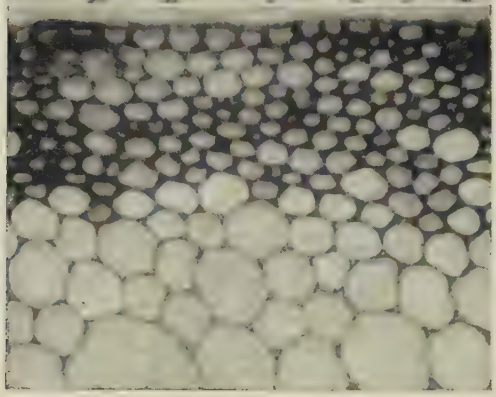


Plate II. Sclerenchymatous ring and lignified parenchyma of basal culm internodes of rye. A: erect plants, dressed with 30 kg N per ha; B: lodged plants, dressed with 140 kg N per ha.

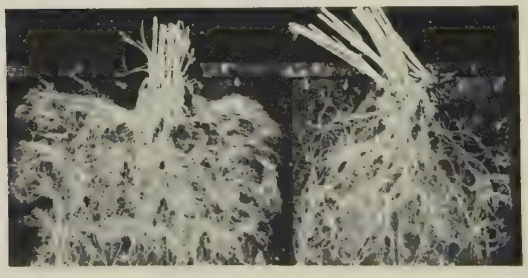


Plate III. Root system of oat plants on pin boards after being washed free from soil. *Left*: erect plants, dressed moderately with nitrogen; *right*: lodged plants, supplied excessively with nitrogen.

sturdy roots. This was confirmed by a number of experiments in 1953 in which root systems of lodged and erect plants have been collected and studied. The root samples were taken according to the method described on page 251 a few weeks before ripening of the crop. At that time the coronal roots of the non-lodged plants which had been supplied with a moderate amount of nitrogen were more vigorous than those of the lodged plants which had been supplied amply with nitrogen (see Plate III and IV and Table VI). They were

TABLE VI

Effect of nitrogen nutrition (lodging) on weight of roots of cereal plants

Field and cereal	Nitrogen supply	Lodged(l) or erect(e)	Yield of roots, g (to a depth of 20 cm)
2. Summer wheat	moderate	e	2.94
	excessive	l	1.18
3. Summer wheat	moderate	e	1.71
	excessive	l	1.04
6. Oats	moderate	e	2.46
	excessive	l	1.57
7. Oats	low	e	2.53
	excessive	e	3.49
	,,	l	1.97
8. Oats	moderate	e	3.97
	excessive	l	1.09

slightly thicker, were much less flexible, had many more branch roots and had a white colour as contrasted with the yellow-brown colour of the roots of lodged plants. Furthermore there existed a pronounced difference in lignification (Table VII). The coronal roots of the lodged oat plants were practically free from lignified cells beneath the epidermis as contrasted with those of the non-lodged plants which had a zone of lignified cells (Plate VA and B). Degree of lignification of the stele was also less pronounced. Lignin as per cent of dry matter was found to be slightly higher in roots of lodged plants. The latter need not be contradictory to the anatomical picture if it is assumed that in the erect plants, in addition to lignin, other C-compounds in even greater quantities have been used to strengthen the tissues.

TABLE VII

Effect of nitrogen nutrition on root characters of oat and wheat plants (coronal roots at 1 cm from culm base).

Cereal and nitrogen supply	Lodged (l) or erect(e)	Number of roots used	Diameter, μ	Diameter of stele, μ	Lignified layer beneath hypodermis			Wall thickness of lignified cells in stele μ	Thickness of inner cell wall of endodermis, μ	Ratio, thickness inner cell wall to width of endodermis
					Number of cell layers	Thickness of layer, μ	Thickness of lignified cell wall, μ			
Oats										
Moderate	e	48	906±21	335±9	2.0±0.17	47±3.5	3.5±0.13	3.0±0.10	6.0±0.22	0.36±0.14
Excessive	l	46	862±28	369±10	0.3±0.13	7±0.3	2.9±0.51	2.2±0.07	3.4±0.25	0.17±0.13
S. wheat										
Moderate	e	16	806±22	341±10	2.9±0.37	70±8.2	3.7±0.45	2.4±0.08	5.6±0.34	0.33±0.03
Excessive	l	16	789±39	323±16	2.1±0.31	45±6.4	1.8±0.27	1.9±0.08	4.0±0.23	0.21±0.02
S. wheat										
Moderate	e	14	894±47	401±22	3.4±0.18	77±3.8	2.9±0.25	2.0±0.15	4.7±0.35	0.25±0.03
Excessive	l	14	888±25	366±11	2.6±0.19	60±3.8	2.2±0.15	1.8±0.11	3.9±0.21	0.19±0.02

A very marked contrast existed in the degree of thickening of the inner cell wall of the endodermis (Plate VC and D).

The loss of most branch roots and also the discolouration indicate that the roots of the lodged plants had been more liable to microbial attack than those of the non-lodged plants which were quite intact. It is probable that the large differences in weight of roots between lodged and erect plants (cf Table VI) are partly due to the more severe attack on the former roots by micro-organisms during the period between flowering and ripening of the crop. That during this period in cereals a decrease in root weight may occur can be seen from the data of Schulze [33]).

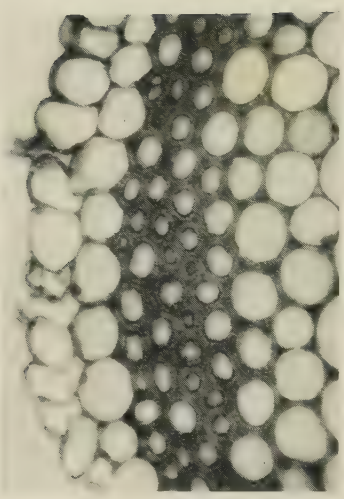
The results of the above-mentioned experiments have shown that weakness of the basal parts of cereal plants in different cases may depend on a poor development of different plant characters. In one case a small diameter of the basal culm internodes will be the limiting factor, in a second a reduced culm wall thickness, a poor lignification of the culm tissues, or a weak root system, while in a third a combination of these factors occurs.

Liability to lodging, however, does not merely depend on weakness of lower culm or root system but on also lack of proportionality between sturdiness of the basal parts of the plant and weight of the

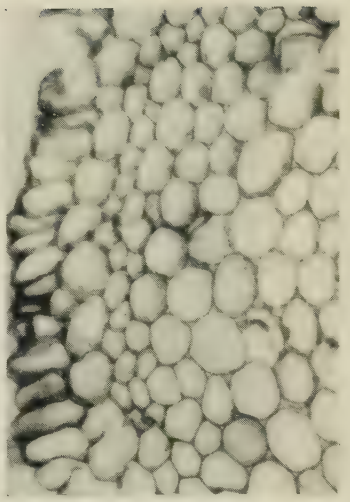
A

B

Plate IV. Culm bases and root systems of oat plants. A : erect plants, supplied moderately with nitrogen. B : lodged plants, supplied excessively with nitrogen.



A



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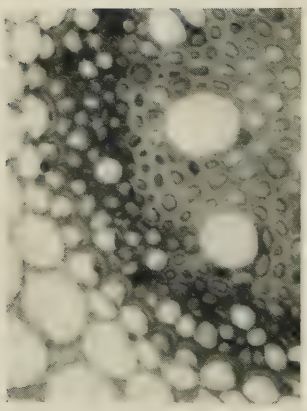
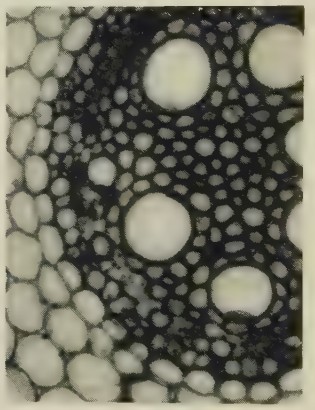


C



D

Plate V. Transverse sections of coronal roots of oats. A and B: epidermis with part of cortex. C and D: stele with endodermis. A and C: moderate nitrogen, erect plants. B and D: excessive nitrogen, lodged plants. The roots of the erect plants possess three lignified cell layers beneath the hypodermis which are absent in the roots of the lodged plants. Furthermore the inner cell walls of the endodermis of the former plants and the walls of the lignified cells of the stele are more thickened than is the case in roots of lodged plants.

upper parts. A crop with relatively strong lower culms and roots may have a high liability to lodging when the plants are long-strawed and have heavily developed upper culm internodes, leaves and ears. On the other hand a plant with relatively weak basal culms and roots may have a low tendency to lodging because of poor development of upper parts and of shortness of straw.

c. *The cause of the nitrogen effect*

The influence of nitrogen nutrition on various plant characters, as described above, may be attributed to a direct physiological

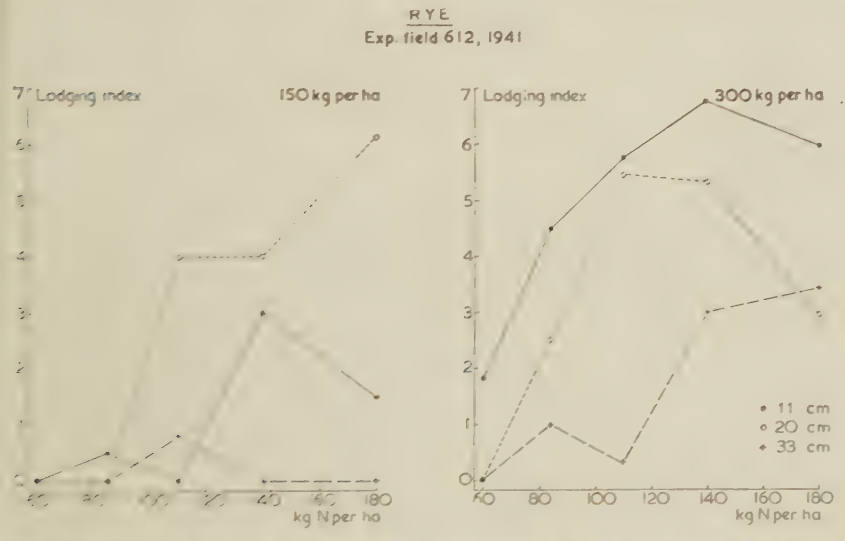


Fig. 2. Effect of rate of seeding (150 and 300 kg per ha), spacing (11, 20 and 33 cm.) and nitrogen nutrition on lodging of winter rye. Lodging indices determined 46 days before harvesting.

effect of nitrogen or to an indirect effect resulting from increased shading of the lower internodes of the culms. An improved nitrogen nutrition favours the stooling of the plants as well as leaf development. Both factors considerably increase the density of the crop. In order to study the direct and indirect effects separately the following experiments have been carried out:

1. Rye and wheat were sown on experimental fields at different rates and at different spacings. By varying the amount of applied

fertiliser nitrogen, it was possible to study the effect of nitrogen at varying degrees of density of the crop.

2. Oats were sown in Mitscherlich pots and supplied with different amounts of nitrogen. A number of pots were exposed to full sunshine in a greenhouse whereas the others were placed in part of the greenhouse where direct sunshine was excluded by using curtains of white paper. Wire frames were used for supporting the leaves in such a way that the exposure to light of the lower internodes was not affected by variations in leaf development resulting from differences in nitrogen nutrition.

1. Field experiments. Winter rye and summer wheat were sown at the rate of 75, 150 and 300 kg per ha at 11, 20 and 33 cm spacing. Nitrogen was applied at the rate of 60, 85, 110, 140 and 180 kg N per ha in 1941 and 0, 40, 80, 120 and 160 kg N per ha in 1942. In both cases ammonium nitrate limestone has been used as the nitrogenous fertiliser.

The winter rye of Exp. 612 (1941) lodged shortly after flowering. Lodging indices have been plotted in Fig. 8. The effect of density of the crop on lodging appeared to be of more importance than that of nitrogen supply. This may be concluded from the fact that a dressing of 180 kg N per ha gave no lodging when the rye had been sown at the rate of 150 kg per ha and at 33 cm spacing, whereas severe lodging occurred at much lower dressings of nitrogen when the stand of the crop was more dense. Similar results have been obtained on Plot 659 with winter rye and on Plot 658 with summer wheat in 1942 (see Fig. 9). On Exp. plot 612 the highest grain yield was obtained at spacings of 20 and 33 cm. At 11 cm grain production was considerably reduced. The rate of seeding had little effect on yield in this experiment. On Exp. plot 658 a spacing of 11 cm gave a marked drop in grain yield when the wheat was sown at 300 kg per ha and when the nitrogen supply was higher than 80 kg per ha. On Exp. plot 659 a spacing of 11 cm gave markedly higher grain yields than one of 33 cm. At 20 cm the grain yields were similar to those at 11 cm. A rate of seeding of 75 kg per ha was inadequate for obtaining an optimal yield on both latter experimental plots. On plot 659, 300 kg gave even higher grain yields than 150 kg notwithstanding the fact that lodging was much more severe at the former rate of seeding (cf Fig. 9). This demonstrates that in this case lodging hardly reduced grain production.

The results of a number of measurements of length and thickness of internodes are plotted in Fig. 10. The effect of excessive nitrogen on length of lower internodes was particularly clear in the wheat plants of Experiment 658 at a rate of seeding of 300 kg per ha. That

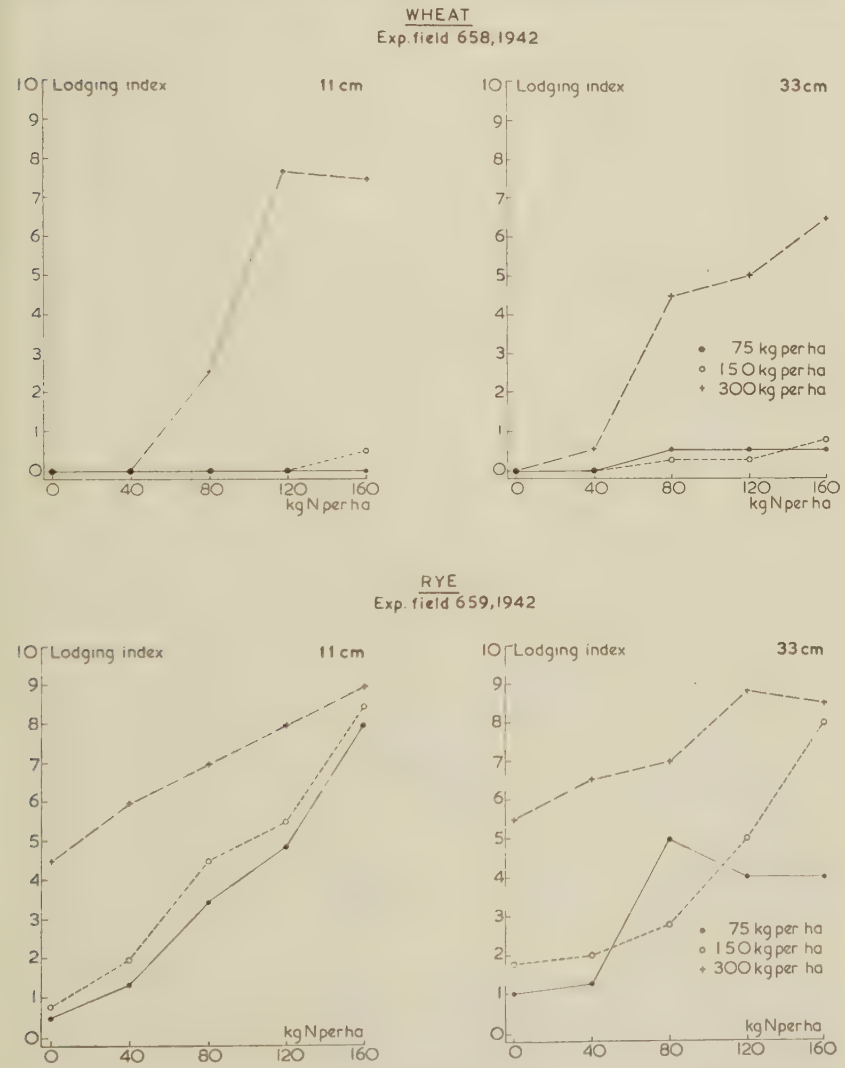


Fig. 9. Effect of rate of seeding (75, 150 and 300 kg per ha), spacing (11 and 33 cm) and nitrogen nutrition on lodging of summer wheat and winter rye. Lodging indices determined 7 days before harvesting.

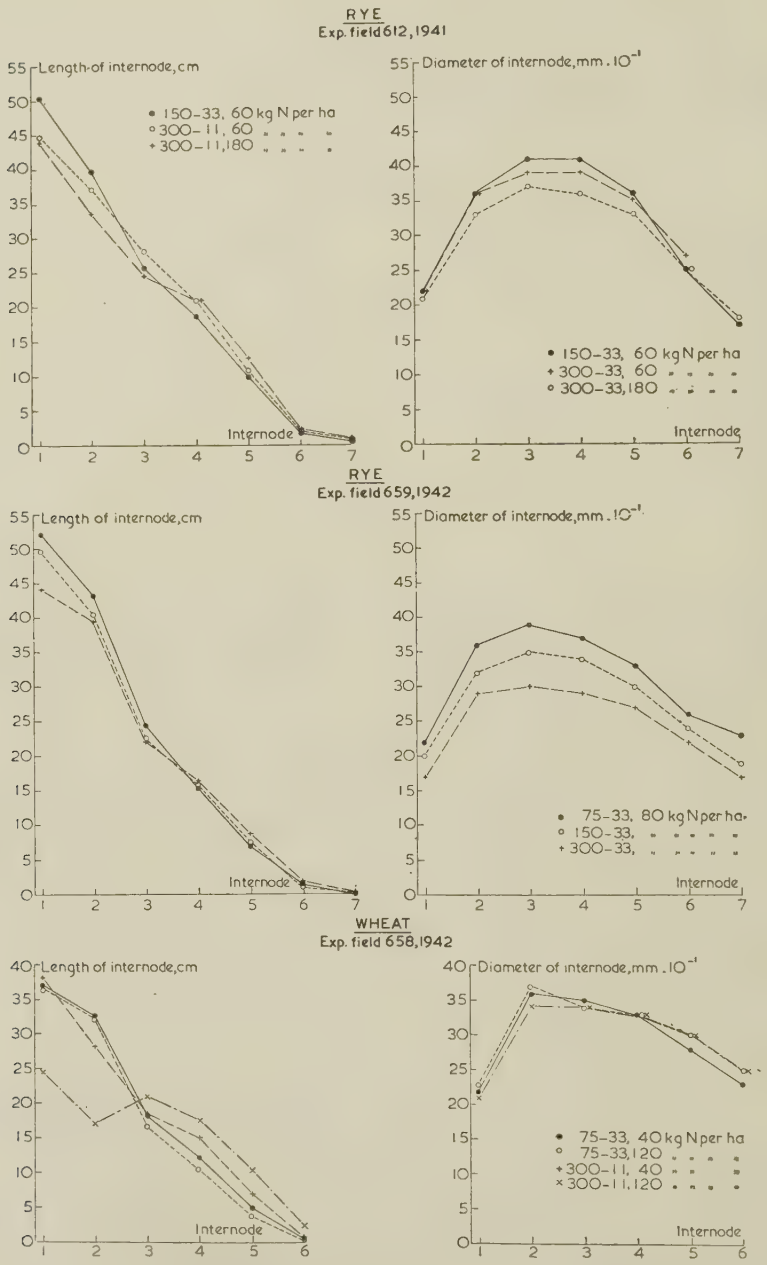

RYE
Exp. field 612, 1941
Length of internode, cm
• 150–33, 60 kg N per ha
○ 300–11, 60 " " " "
+ 300–11, 180 " " " "
Internode
Diameter of internode, mm . 10⁻¹
• 150–33, 60 kg N per ha
+ 300–33, 60 " " " "
○ 300–33, 180 " " " "
Internode
RYE
Exp. field 659, 1942
Length of internode, cm
Internode
Diameter of internode, mm . 10⁻¹
• 75–33, 80 kg N per ha
○ 150–33, " " " "
+ 300–33, " " " "
Internode
WHEAT
Exp. field 658, 1942
Length of internode, cm
Internode
Diameter of internode, mm . 10⁻¹
• 75–33, 40 kg N per ha
○ 75–33, 120 " " " "
+ 300–11, 40 " " " "
× 300–11, 120 " " " "
Internode

Fig. 10. Effect of rate of seeding (75, 150 and 300 kg per ha), spacing (11 and 33 cm) and nitrogen nutrition on length and diameter of culm internodes of winter rye and summer wheat. 1st = highest internode. For lodging indices see Tables VIII and IX.

this effect was indirect, resulting from shading of the lower internodes through increased stooling and leaf formation, may be concluded from the fact that plants sown at a rate of seeding of 75 or 150 kg per ha and at a spacing of 33 cm did not possess longer lower internodes when dressed with excessive nitrogen. Apparently in the latter case the increased leaf formation was inadequate to prevent the exposure to direct sunlight of the lower internodes.

Similarly plants with equal nitrogen dressings possessed considerably longer lower internodes when the density of the crop was greater because of a higher rate of seeding or a narrower spacing.

In the case of the rye plants of Experiments 612 and 659 density of crop and nitrogen nutrition exerted only a slight effect on the length of the lower internodes. The number of internodes tended to increase with increased density of the crop. As a result of this, higher values for the lower internodes may be found in the more densely sown crops of the latter experiments when average values for all culms per sample are calculated (cf footnote on p. 263).

Culm diameter of the lower internodes of rye plants was considerably reduced by an increased rate of seeding on Exp. plot 659. This may have been the main cause of the differences in lodging between plots of different density. In the case of Exp. 612 (rye) and Exp. 658 (wheat), however, reduced culm diameter cannot have been responsible for the increased lodging of crops with a higher density or with an increased nitrogen supply as practically no effect of these conditions on culm diameter was observed (see Fig. 10).

Weight per unit of culm length was considerably reduced by increased density of the crop in the case of Exp. 658 (wheat) and of Exp. 659 (rye) but not on Exp. 612 (Table VIII). In the wheat plants it was apparently due partly to the thicker culm wall of the less densely sown plants. A slight effect of nitrogen nutrition on culm wall thickness was noted in the rye of Exp. 612 as well as in the wheat of Exp. 658 (Table IX).

No clear relationship between density and nitrogen nutrition of the crop and extension of sclerenchymatous tissue was observed in the rye plants of Exp. 612. In the case of the wheat of Exp. 658 the lodged plants of the densely sown crop (300–11) treated excessively with nitrogen had a thinner sclerenchyma ring than plants sown under less dense conditions (75 33). The area of lignified tissue of

TABLE VIII

Effect of nitrogen nutrition, rate of seeding and spacing of cereal plants on weight per cm of culm length of second lowest internodes

Cereal *), exp., year and harvest date	Rate of seeding, kg per ha	Spacing, cm	Kg N per ha	Lodging index		Weight per cm of culm length, mg		
				date	date	5 **)	6 **)	7 **)
Winter rye,				*21.6*	*18.7*			
612, 1941,	150	33	60	0	2	—	18.7±1.1	19.0±3.0
Aug. 5	150	33	180	0	3	14.1±1.0	16.0±1.0	—
	150	11	60	0	3	12.0±1.5	18.1±0.9	15.7±1.7
	150	11	180	1½	6	—	14.5±0.8	16.5±1.4
	300	33	60	0	4½	—	13.9±0.1	14.4±0.1
	300	33	180	3½	7	14.1±1.8	18.0±1.3	—
	300	11	60	2	8	—	17.2±0.2	—
Winter rye,				*18.7*	*12.8*			
659, 1942,	75	33	80	6	5	15.5±0.9	18.3±0.8	20.3±3.6
Aug. 18	75	11	80	3	3½	15.2±0.7	20.0±0.8	22.0±0.9
	150	33	80	5	3	—	15.0±0.7	11.4±1.1
	300	33	80	8½	7	9.9±1.2	12.4±0.5	12.5±0.8
	300	11	80	8½	7	—	10.7±0.5	9.0±1.1
Summer				*14.7*	*28.8*			
wheat, 658,	75	33	40	½	0	19.0±0.7	20.9±1.8	—
1942, Sept. 3	75	33	120	0	½	18.0±1.0	23.6±0.9	—
	150	33	40	0	0	15.3±0.8	17.5±0.9	—
	150	33	120	0	2½	15.6±0.7	16.5±1.0	—
	300	11	120	9	8	13.8±1.1	12.7±0.2	—

*) Culms collected: Exp. 612 two weeks, Exp. 659 four weeks, Exp. 658 one week before harvesting.

**) Culms with 5, 6 and 7 internodes respectively.

the sclerenchymatous zone was also reduced in the densely sown wheat plants.

Thickness of sclerenchyma cell walls was reduced by increased density of the crop. It was slightly affected by increased nitrogen nutrition in the case of the rye plants but not in the case of the wheat (cf Table IX).

2. Pot experiment with oats. In this experiment the combined effect of potassium supply, nitrogen nutrition and illumination of the plants on growth and yield of oats has been studied. Although a full report of the results of this experiment will be given elsewhere, the measurements of those plant characters which are related to tendency to lodging will be recorded in this paper.

TABLE IX

Effect of nitrogen nutrition, rate of seeding and spacing on culm wall thickness and anatomical characteristics of the second lowest culm internodes

Cereal, exp., year, harvest date	Rate of seeding, kg per ha	Spacing, cm	Kg N per ha	Lodging index		Number of culms used	Number of internodes per culm	Culm wall thickness, μ	Thickness of sclerenchymatous ring, μ		Lignified tissue as % of total area of scl. ring	Thickness of sclerenchyma cell walls μ,	Number of vascular bundles
				date	date				A **)	B **)			
				21.6	*18.7*								
Winter rye,	150	33	60	0	2	9—17	6	687 ± 17	83 ± 2	130 ± 5	75 ± 3	5.3 ± 0.16	25 ± 0.8
612, 1941,						6—7	7 *)	701 ± 59	80 ± 4	136 ± 6	66 ± 4	5.3 ± 0.24	23 ± 1.8
Aug. 5	150	33	180	0	3	4—16	5	543 ± 16	78 ± 3	118 ± 3	84 ± 2	4.4 ± 0.34	23 ± 1.7
						12—13	6	659 ± 29	87 ± 2	129 ± 4	73 ± 4	5.0 ± 0.20	26 ± 0.5
	300	33	60	0	4½	23—27	6	617 ± 22	78 ± 2	123 ± 3	77 ± 2	4.7 ± 0.17	24 ± 0.5
						3	7	604 ± 23	75 ± 3	119 ± 5	68 ± 4	4.8 ± 0.22	26 ± 2.0
	300	33	180	3½	7	7—8	5	565 ± 18	89 ± 5	135 ± 5	76 ± 6	4.4 ± 0.22	21 ± 0.8
						17—18	6	623 ± 24	89 ± 3	140 ± 4	68 ± 2	4.7 ± 0.16	25 ± 0.5
	300	11	60	2	8	10	6	640 ± 25	92 ± 8	141 ± 8	70 ± 6	4.1 ± 0.25	24 ± 3.5 †)
				14.7	*28.8*								
Summer wheat,	75	33	40	½	0	20—30	5	907 ± 28	81 ± 3	127 ± 3	87 ± 2	6.1 ± 0.09	29 ± 0.6
658, 1942,	75	33	120	0	½	21—24	5	878 ± 31	77 ± 3	132 ± 3	88 ± 2	6.3 ± 0.17	29 ± 0.6
Sept. 3						3—4	6	969 ± 57	83 ± 8	141 ± 3	88 ± 7	6.1 ± 0.27	34 ± 1.0
	150	33	40	0	0	21—27	5	734 ± 26	85 ± 3	129 ± 3	98 ± 0	6.0 ± 0.16	31 ± 0.7
	150	33	120	0	2½	11—23	5	686 ± 40	77 ± 2	119 ± 3	90 ± 2	6.2 ± 0.19	30 ± 0.6
	300	11	120	9	8	10—13	5	696 ± 35	68 ± 2	118 ± 4	85 ± 4	4.8 ± 0.21	30 ± 0.8
						14—17	6	737 ± 26	67 ± 2	117 ± 4	79 ± 2	5.0 ± 0.14	30 ± 0.6

*) Third lowest internodes used.

**) A = no vascular bundle, B = vascular bundle inside sclerenchymatous ring.

†) Three culms only used.

The Mitscherlich pots used contained approximately 5 kg of a potassium-deficient sandy soil of pH 5.2. Potassium was supplied in amounts of 0.5, 1.0 and 3.0 g K_2SO_4 per pot, nitrogen in amounts of 175, 350 and 1050 mg N per pot in the form of either calcium nitrate or ammonium sulphate. Further dressings consisted of monocalcium phosphate, magnesium sulphate and copper sulphate.

There was a considerable difference between oats growing in the unshaded and those in the shaded part of the greenhouse. In both cases the plants responded to the K-dressings. The requirement for nitrogen of the unshaded plants was considerably higher than that of the shaded ones, indicating a difference in the rate of carbon dioxide assimilation. The highest applications of nitrogen in the form of ammonium sulphate depressed the yield in the case of the shaded plants.

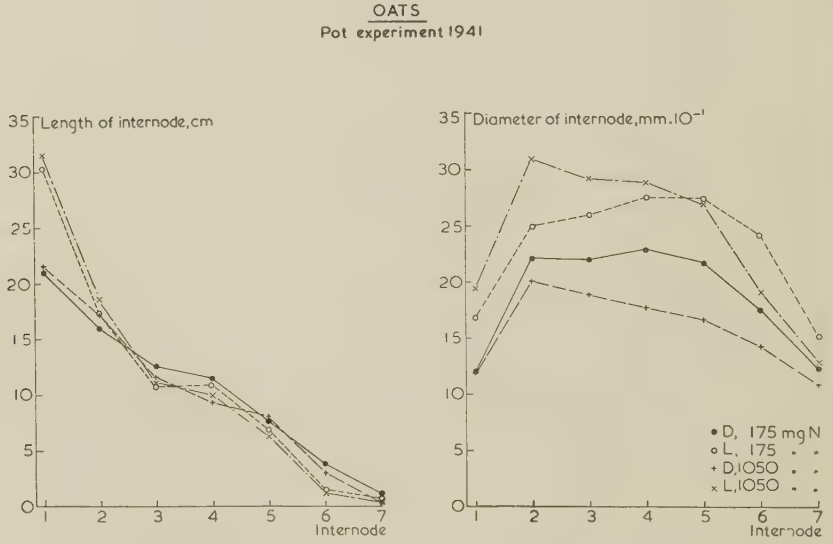


Fig. 11. Effect of illumination and nitrogen nutrition on length and diameter of internodes of oat culms. N in the form of ammonium sulphate. D = shaded, L = unshaded, 1st = highest internode.

The effect of nitrogen nutrition and exposure to light on length of internodes is demonstrated in Fig. 11. It will be seen that the length of the lower internodes was not increased by the nitrogen dressings. Shading, however, resulted in the formation of considerably longer lower internodes than were found in plants exposed to bright sunshine. In agreement with the results of the above-mentioned field experiments 612, 658 and 659, this pot experiment shows that the elongation of the lower internodes of cereal plants

as often observed in nitrogen-dressed fields is not a direct effect of improved nitrogen nutrition but is due to an indirect shading effect.

The negative correlation between length of lower and upper internodes as observed more or less clearly in the above-mentioned field experiments again is found in this pot experiment. Shaded plants have considerably shorter upper internodes than unshaded ones.

The number of internodes was not increased by shading or by increased nitrogen supply. Generally it was somewhat higher in the illuminated plants. This is in contrast with the results obtained on a number of experimental fields. Plants supplied with ammonium sulphate tended to have more internodes than those with calcium nitrate.

Culm diameter was considerably reduced in the shaded plants as compared with the unshaded ones (Fig. 11). This was the case with both upper and lower internodes. Excessive amounts of ammonium sulphate likewise reduced the internode diameter throughout the culm in the shaded plants. In the unshaded plants the diameter of the basal internodes was reduced but that of the higher ones was increased by excessive amounts of ammonium sulphate. Calcium

TABLE X

Effect of nitrogen nutrition and illumination of oat plants on weight per cm of culm length of second lowest internodes (pot experiment 1941)

Nitrogen		Illumination	Weight per cm of culm length, mg	
mg per pot	compound		6 ***)	7 ***)
175	as *)	D **)	4.1 ± 0.2	4.1 ± 0.1
175	as	L	—	7.1 ± 0.3
350	as	D	3.6 ± 0.2	3.7 ± 0.2
350	as	L	—	7.8 ± 0.2
1050	as	D	3.8 ± 0.3	3.4 ± 0.2
1050	as	L	7.2 ± 0.3	7.0 ± 0.2
175	cn	D	4.0 ± 0.1	3.9 ± 0.1
175	cn	L	—	7.3 ± 0.2
350	cn	D	4.4 ± 0.2	5.1 ± 0.4
350	cn	L	—	8.0 ± 0.2
1050	cn	D	4.9 ± 0.2	4.4 ± 0.4
1050	cn	L	7.3 ± 0.4	8.2 ± 0.3

*) as = ammonium sulphate, cn = calcium nitrate.
**) D = shaded, L = unshaded.
***) Culms with 6 and 7 internodes respectively.

nitrate gave similar results in this respect both in shaded and unshaded plants but the differences were less striking.

Weight per cm of culm length was much lower in the shaded plants than in those grown in sunlight. This was due partly to reduced culm diameter, partly to reduced culm wall thickness and partly to reduced lignification of the lower internodes (see Tables X and XI). In the shaded plants increasing amounts of nitrogen in the form of ammonium sulphate caused a slight reduction in culm weight.

Culm wall thickness was markedly reduced by shading of the plants. Excessive amounts of nitrogen accentuated this effect. In the unshaded plants high amounts of nitrogen tended to increase the culm wall thickness (Table XI).

Rate of lignification of the culms was determined microscopically in transverse sections as well as chemically. Both thickness of sclerenchymatous layer and thickness of the sclerenchyma cell walls were found to be considerably reduced by shading of the plants as well as by increased nitrogen supply. The results of the chemical analyses were in general agreement with the microscopical observations (cf Tables XI and XII).

Excessive nitrogen has reduced the lignin content of shaded plants to a much higher degree than that of unshaded plants.

TABLE XI

Effect of nitrogen nutrition and illumination on culm wall thickness and anatomical characteristics of the second lowest culm internodes of oat plants (pot experiment 1941)

N *) mg per pot	Illumination	Number of culms used	Number of internodes per culm	Culm wall thickness, μ	Thickness of sclerenchymatous ring, μ		Lignified tissue as % of total area of scl. ring	Thickness of sclerenchyma cell walls, μ	Number of vascular bundles
					A †)	B †)			
175	D **)	8	6	466±18	41±2	88±1	51±4	2.0±0.10	16±0.8
		23–28	7	430±6	41±2	91±2	53±3	2.1±0.09	18±0.3
175	L	33–34	7	479±11	47±1	97±2	63±2	3.3±0.07	22±0.4
1050	D	2–4	6	472±14	38±6	90±0	59±9	2.2±0.15	14±0.3
		9–14	7	394±12	32±2	78±4	50±3	1.5±0.18	19±0.5
1050	L	7	6	520±15	47±3	99±4	46±2	2.8±0.33	20±0.6
		24–28	7	497±20	43±1	91±4	54±2	2.7±0.07	21±0.6

*) as $(NH_4)_2SO_4$.

**) D = shaded, L = unshaded.

†) A = no vascular bundle, B = vascular bundle inside sclerenchymatous ring.

The number of vascular bundles was slightly reduced by shading the plants (Table XI).

TABLE XII

Effect of nitrogen nutrition and illumination on lignin content of oat culms (pot experiment 1941)

Nitrogen		Illumi-	Lignin in internodes, % of dry matter †)		
mg per pot	compound	nation	5th	4th	3rd
175	as *)	D **)	20.8	22 6	22.3
175	,,	L	21.7	22.0	22.2
1050	,,	D	7.9	16.9	17.0
1050	,,	L	21.2	23.4	23.1
175	cn	D	18.6	19.9	19.5
175	,,	L	22.1	21.9	21.4
1050	,,	D	10.5	11.3	14.5
1050	,,	L	20.8	22.7	22.9

*) as = ammonium sulphate, cn = calcium nitrate.
**) D = shaded, L = unshaded.
†) averages of duplicate values.

The results of the field and pot experiments recorded in this section show that the unfavourable effect of excessive nitrogen on the strength of the lower internodes of cereal plants is due partly to an indirect shading effect resulting from an abundant leaf formation and partly to a direct nutritional effect. Elongation of the lower internodes depends entirely on the shading effect. Reduction of culm diameter, of culm wall thickness and of lignification may be brought about by shading as well as by a direct nitrogen effect.

5. EFFECT OF POTASSIUM NUTRITION

The effect of potassium nutrition on lodging has been studied on a number of experimental fields with rye, barley and wheat. The soils on which these experiments had been laid out, were in general poor in potassium so that plant growth was reduced considerably by K-deficiency when potassium dressings were omitted. The influence of K-supply on lodging was tested by applying increasing amounts of nitrogenous fertilisers at different K-levels: no K, moderate, normal and excessive amounts of added potassium salts respectively.

Although in some cases the plants dressed with potassium lodged more severely than those without a K-dressing (Fig. 12), this was probably due to the fact that the latter suffered from potassium

deficiency so that a far less heavy and dense crop was formed. The straw of potassium-deficient plants appeared to be more brittle as a result of which breaking of the culms occurred much more frequently than was the case with fully dressed plants. These breakages

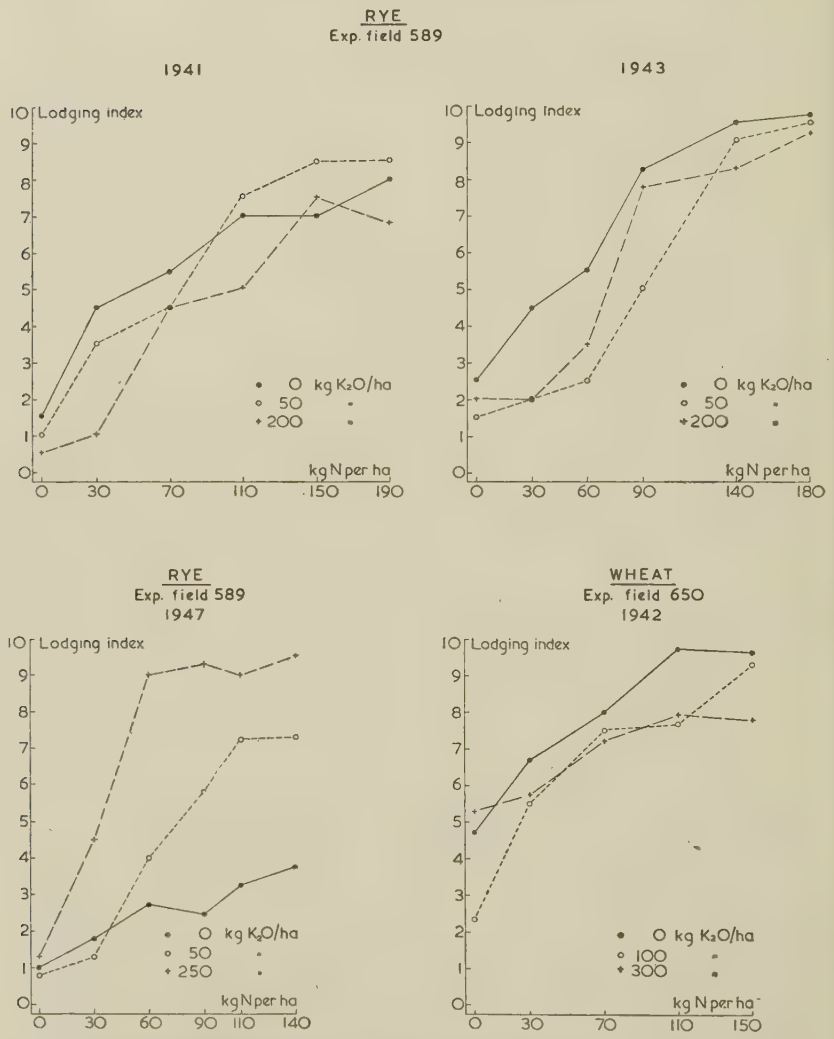


Fig. 12. Effect of potassium and nitrogen nutrition on lodging of winter rye (in three different years) and of summer wheat. Lodging indices determined 14 (Exp. 589, 1941), 11 (Exp. 589, 1943), 20 (Exp. 589, 1947) and 35 (Exp. 650, 1942) days respectively before harvesting.

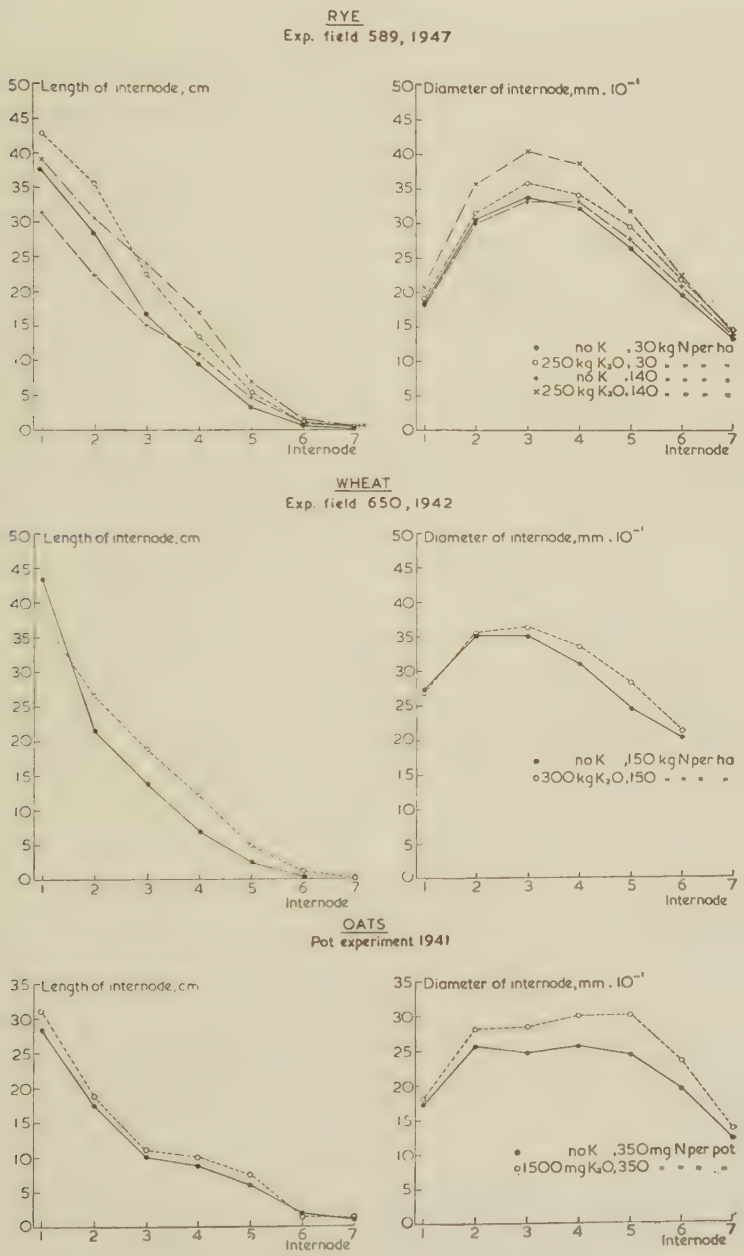

RYE
Exp. field 589, 1947
Length of internode, cm
Diameter of internode, mm . 10⁻¹
Internode
no K , 30 kg N per ha
250 kg K₂O, 30 - - - -
no K , 140 - - - -
250 kg K₂O, 140 - - - -
WHEAT
Exp. field 650, 1942
Length of internode, cm
Diameter of internode, mm . 10⁻¹
Internode
no K , 150 kg N per ha
300 kg K₂O, 150 - - - -
OATS
Pot experiment 1941
Length of internode, cm
Diameter of internode, mm . 10⁻¹
Internode
no K , 350 mg N per pot
1500 mg K₂O, 350 - - - -

Fig. 13. Effect of potassium nutrition on length and diameter of culm internodes of winter rye, summer wheat and oats. For lodging data see Figure 12.

TABLE XIII

Effect of potassium nutrition of cereal plants on weight per cm of culm length

Cereal *), experiment and soil	K_2O, kg per ha, or mg per pot	Nitrogen kg per ha or mg per pot	Nitrogen compound	Illumination	Weight per cm of culm length, 2nd lowest internode **), mg		
					5	6	7
Oats, pot exp., 1941, sandy	0	350	as ***)	D †)	—	—	3.1±0.2
	0	350	,,	L	—	—	5.5±0.2
	0	350	cn	D	—	3.2±0.1	—
	0	350	,,	L	—	5.5±0.4	5.3±0.2
	1500	350	as	D	—	3.6±0.2	3.7±0.2
	1500	350	,,	L	—	—	7.8±0.2
	1500	350	cn	D	—	4.4±0.2	5.1±0.4
	1500	350	,,	L	—	—	8.0±0.2
Wheat, field exp. 650, 1942, sandy	0	0	—	—	14.3±1.0	18.1±1.4	—
	0 (100) **)	0	—	—	13.6±0.8	16.6±0.7	—
	100 (300)	0	—	—	14.2±0.8	15.1±1.0	—
	300 (600)	0	—	—	12.6±0.5	15.7±1.5	—
	0	150	anl	—	15.3±0.8	13.3±0.9	—
	0 (100)	150	,,	—	14.9±0.8	14.6±1.1	—
	100 (300)	150	,,	—	12.8±1.3	14.2±1.1	—
	300 (600)	150	,,	—	15.6±1.6	14.7±0.5	11.8±0.3

*) Oat culms collected when the plants were ripe, wheat culms four weeks before harvesting.

**) Figures in brackets refer to K-dressings in 1941.

***) as = ammonium sulphate, cn = calcium nitrate, anl = ammonium nitrate limestone.

† D = shaded, L = unshaded.

†† Culms with 5, 6 and 7 internodes respectively.

occurred not only at the lower internodes but also at higher ones. When a comparison was made between plants treated with a moderate and an excessive amount of potassium, no difference in lodging could be detected. This does not indicate a strengthening effect of large amounts of potassium on the culm of cereals as is sometimes stated in the literature [35]. It is an agreement with the results obtained by Krantz and Chandler [23] in field experiments with maize.

The effect of K-nutrition on various plant characters related to standing ability of cereal plants is given in Tables XIII–XV and in Fig. 13. It will be seen that K-deficient plants in general had shorter internodes than plants treated amply with potassium. This applies to the lower as well as to the upper internodes (Fig. 13).

TABLE XIV

of potassium nutrition on wall thickness and anatomical characteristics of the second lowest culm internodes

Exp. and year	Kg K_2O per ha	Kg N per ha	Lodged (l) or erect(e)	Number of culms used	Number of internodes per culm	Culm wall thickness, μ	Thickness of sclerenchymatous ring, μ A †)	Thickness of sclerenchymatous ring, μ B †)	Lignified tissue as % of total area of sclerenchymatous ring	Thickness of sclerenchyma cell walls, μ	Number of vascular bundles
589, 1947	0	140	e	60	—	545 ± 14	62 ± 1	—	—	2.4 ± 0.08	—
	250	140	l	59—60	—	726 ± 17	64 ± 1	—	—	2.5 ± 0.10	—
650, 1942	0	150	l	13—14	5	779 ± 31	89 ± 4	132 ± 4	90 ± 2	4.7 ± 0.25	24 ± 0.7
				5—12	6	715 ± 40	98 ± 3	149 ± 6	88 ± 3	4.5 ± 0.27	27 ± 1.2
	[illegible]	[illegible]	l	22—24	7	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
				44—48	6	724 ± 20	90 ± 3	130 ± 3	81 ± 2	5.2 ± 0.13	26 ± 0.8

collected: Exp. 589 two weeks, Exp. 650 four weeks before harvesting.
ascular bundle, B: vascular bundle inside sclerenchymatous ring.

TABLE XV

Effect of potassium nutrition of cereal plants on lignin content of lower culm internodes

Cereal	Experiment, year and soil	Kg K_2O applied per ha	Kg N per ha	Lodged(l) or erect(e)	Lignin, % of dry matter
Winter rye †)	589, 1947, sandy	0	0	e	25.5 ± 0.35
		250	0	e	19.3 ± 0.07
		0	30	e	22.2 ± 0.14
		250	30	e	19.3 ± 0.28
		0	140	l **)	22.8 ± 0.31
		250	140	l	16.0 ± 0.12
Summer wheat ††)	650, 1942, peaty	0	0	e	18.4 ± 0.15
		0 (100) *)	0	e	17.1 ± 0.10
		100 (300)	0	e	11.3 ± 0.32
		300 (600)	0	e	15.7 ± 0.17
		0	150	l	18.2 ± 0.57
		0 (100)	150	l	17.5 ± 0.68
		100 (300)	150	l	16.4 ± 0.16
		300 (600)	150	l	14.3 ± 0.43

†) Second lowest internodes, collected two weeks before harvesting.
††) Third lowest internodes, collected four weeks before harvesting.
*) Figures in brackets refer to K-dressings in 1941.
**) Lodging index = 5.

Culm diameter was clearly reduced in potassium-deficient plants.

Weight per cm of basal culm was lower in K-deficient oats than in plants with a normal K-supply (pot experiment 1942). This was apparently due to the reduced culm diameter of the potassium-deficient plants (Table XIII). In the case of wheat K-deficient culms were slightly heavier than those treated with potassium. This may have been due to the somewhat thicker culm walls and the somewhat thicker sclerenchyma zone in the K-deficient plants. In the rye plants of Exp. 589 potassium deficiency gave a highly significant reduction of culm wall thickness (Table XIV).

Thickness of lignified cell walls tended to be slightly reduced in the case of potassium deficiency.

The effect of potassium on lignin content of basal culm internodes is demonstrated in Table XV. In general the plants with the lowest potassium supply have the highest lignin content.

6. EFFECT OF PHOSPHORUS NUTRITION

The effect of phosphorus on the standing ability of cereal plants has been studied on some experimental fields laid out on P-deficient

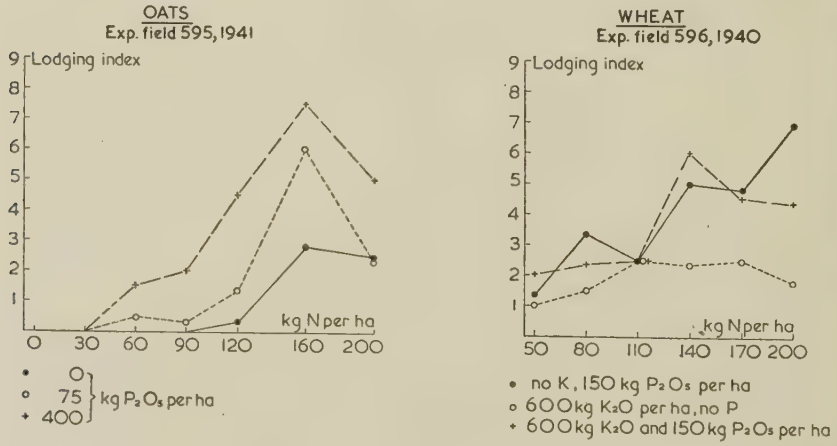


Fig. 14. Effect of phosphorus and nitrogen nutrition on lodging of oats and summer wheat. Lodging indices determined 15 (Exp. 595) and 42 (Exp. 596) days respectively before harvesting.

soils. On these areas increasing amounts of nitrogenous fertilisers were applied at different P-levels in the soil. From the results of

these field experiments as well as from those of pot experiments no particular effect of phosphorus supply on the standing capacity of the plants could be observed. The P-deficient plants lodged less severely than those dressed amply with phosphate apparently due to a poorer development (Fig. 14).

The effect of phosphorus deficiency on anatomical characters was studied in oat and wheat plants grown in a pot experiment. Since the soil used in this experiment was extremely poor in available phosphorus, plants treated with moderate and high amounts of fertiliser phosphorus were investigated. The yields of the phosphorus-deficient wheat plants were approximately 30% of the yields of plants dressed with adequate phosphorus. In the case of oats these figures were 30% (at 0.6 g phosphate per pot) and 60% (at 1.0 g phosphate).

Culm wall thickness was clearly reduced in the phosphorus-deficient plants. In oats this was only the case at the lowest nitrogen level (see Table XVI).

Thickness of the sclerenchymatous ring was likewise reduced in the phosphorus-deficient wheat plants but not in the oat plants. Thickness of the sclerenchyma cell walls was unaffected by the phosphorus supply.

Number of vascular bundles, however, was significantly reduced

TABLE XVI

t of phosphorus nutrition on wall thickness and anatomical characteristics of the lower internodes of oat and wheat plants

Ca-$(H_2PO_4)_2$ g per pot	Nitrogen, *) g per pot	Number of culms used	Diameter of internodes	Culm wall thickness, μ	Thickness of sclerenchymatous ring, μ		Lignif. tissue as % of total area of scl. ring	Thickness of sclerenchyma cell walls, μ	Number of vascular bundles
					A **)	B **)			
0.6	0.350	17—18	33.8±0.2	549±22	75±3	106±4	93±1	5.1±0.11	21±0.7
0.6	1.050	18—20	30.3±0.1	532±23	53±2	104±5	98±1	5.0±0.19	20±0.5
1.0	0.350	14—20	36.7±0.1	518±17	64±2	107±3	94±1	5.7±0.22	22±0.7
1.0	1.050	11—20	37.6±0.1	599±13	63±1	114±3	91±2	5.8±0.21	21±0.4
5.0	0.350	21	39.5±0.1	647±23	81±3	109±3	85±1	5.1±0.17	27±0.5
5.0	1.050	22	38.6±0.1	562±19	68±3	116±3	76±3	3.9±0.23	27±0.3
1.0	0.175	16—20	18.7±0.1	638±24	61±2	102±3	97±0	5.5±0.23	22±0.6
1.0	0.350	10—22	18.2±0.1	566±18	63±2	110±7	100±1	6.0±0.28	21±0.5
5.0	0.175	19—21	34.2±0.0	786±25	85±2	120±3	87±5	5.3±0.09	31±0.4
5.0	0.350	12—20	35.4±0.0	721±30	81±2	125±2	88±2	6.2±0.14	32±0.3

H_4NO_3. **) A: no vascular bundle B: vascular bundle inside sclerenchymatous ring.

in phosphorus-deficient wheat and oat plants. This effect is very remarkable since the number of vascular bundles of cereal culms is in general very constant.

7. EFFECT OF SOIL-pH

Raising the pH of acid soils by liming often results in an improvement in the growing conditions of the plants so that a heavier crop will develop which is more liable to lodging than the unlimed one. This was found to be the case on an acid peaty soil where relatively large amounts of soil nitrogen became available upon liming (Fig. 15).

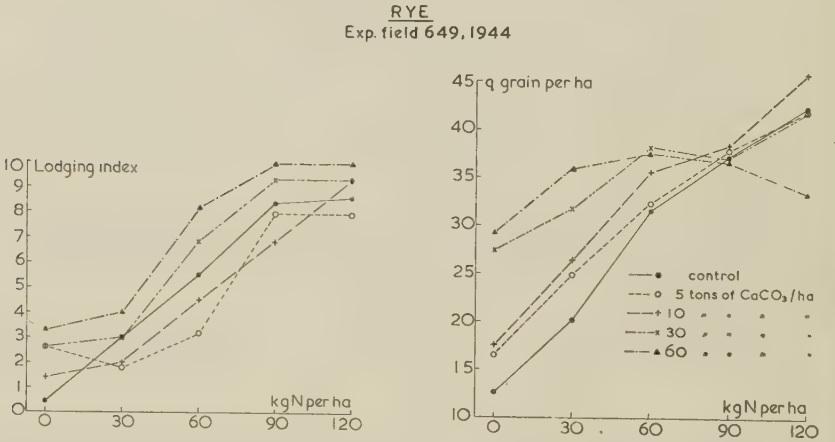


Fig. 15. Effect of liming an acid low moor peat soil and nitrogen dressings on yield and lodging of winter rye. Lodging indices determined 21 days before harvesting.

8. EFFECT OF SOIL STRUCTURE

The effect of soil structure on lodging of cereal crops was studied on a clay soil on which wheat was grown following two different crops, viz. Brussels sprouts leaving a poor soil structure, and red clover leaving an excellent structure. No lodging occurred on the soil with the poor structure notwithstanding the high yields which were obtained at the highest nitrogen dressings. Following the clover a moderate lodging occurred (Table XVII). From the yield data it can be seen that the latter was presumably a result of the improved nitrogen supply owing to nitrogen fixation by the clover.

TABLE XVII

Effect of preceding crop on yield *) and lodging of summer wheat. Field experiment 813, 1944 (date of harvesting Aug. 24)

Kg fertiliser N per ha	After clover (good soil structure)			After Brussels sprouts (poor soil structure)		
	Grain, q**) per ha	Straw, q per ha	Lodging index, Aug. 11	Grain, q per ha	Straw, q per ha	Lodging index, Aug. 11
0	53.6	84.3	0	28.6	37.7	0
40	56.8	92.3	1	38.7	55.4	0
60	55.1	89.3	0	41.9	61.1	0
80	54.2	92.3	2	46.7	66.3	0
100	53.2	89.5	3	47.7	68.2	0
120	51.2	94.0	5½	49.3	71.4	0
140	48.2	88.7	6½	49.1	71.5	0

*) Average values for three plots.
**) 1q = 100 kg.

These results are in agreement with field observations. Lodged areas in unlodged fields may frequently be found to have a better soil structure as a result of which the soil-nitrogen supply to the crop has been more favourable than on the unlodged areas.

When soil structure is extremely poor, anchorage of the roots may be inadequate as a result of which the standing ability of the plants will be reduced. Nevertheless lodging does not occur on such soils because of the poor development of the tops.

9. EFFECT OF LODGING ON YIELD

The yield depressions resulting from lodging depend a) on the growing stage at which the crop lodged and b) on the weather conditions prevailing after lodging has taken place. When the crop lodges before flowering *i.e.* before the plants have reached their full length, the culms may regain their upright position through intercalar growth of the nodes. Although such a crop will easily be flattened again, it may hold its upright position when favourable weather conditions prevail until ripening. Under these circumstances yield depressions will be of less importance than in the case of adverse weather conditions which often bring about a complete flattening. The ears may now remain partly deaf and the kernels formed will be shrivelled.

When the crop lodges some time after flowering the ears will not regain their upright position. Although in this case grain number is

TABLE XVIII

Number of plants and yield of lodged and standing areas in general fields *)							
Field, year and soil	Crop	Lodged(l) or erect(e)	Number of culms per m²	Yield, q per ha		Grain as % of total yield	Weight of 1000 grains, g
				Grain	Straw		
1, 1943, peaty	summer wheat	e	318	43.0	97.1	30.7	—
		l	337	26.7	104.1	25.1	—
2, 1953 sandy	summer wheat	e	560	47.5	76.7	38.2	44.5
		l	595	33.2	77.5	29.9	32.3
3, 1953 sandy	summer wheat	e	508	47.9	85.0	35.6	44.0
		l	550	37.9	80.0	31.6	32.0
4, 1953 sandy	summer wheat	e	540	55.0	92.5	37.2	45.3
		l	510	31.0	65.0	32.2	34.2
5, 1953 sandy	oats	e	383	46.3	57.5	44.4	32.1
		l	418	39.5	55.0	41.6	22.3
6, 1953 sandy	oats	e	—	44.8	56.5	44.2	36.1
		l	—	17.8	61.8	22.4	17.3

*) Border effect eliminated.

not affected, grain weight may be considerably reduced. The degree of reduction likewise depends on weather conditions prevailing after the crop has lodged.

For estimating the reduction in grain yield resulting from lodging the following methods have been employed:

a. A comparison was made between the yields of lodged and non-lodged areas in the same plot. Table XVIII gives examples of such a comparison in crops of summer wheat and oats. Although this method provides an approximate estimation of yield depression, the values obtained may be too low because of the fact that the growing conditions for the non-lodged plants have often been less favourable than those for the lodged plants. Therefore the yield of the standing areas may be considerably lower than the yield which would have been obtained if the plants on the lodged areas had remained unlodged. This may be seen from the results obtained on experimental plots on which different amounts of fertiliser nitrogen had been applied (Fig. 3). If the severely lodged plots of Exp. 589, 1943 supplied with 180 kg N per ha are compared with the slightly lodged plots dressed with 140 kg N per ha, which yielded 4730 kg of rye per ha, yield reductions of 410, 1000 and 1510 kg respectively for the triplicate plots will be found. Compared with the unlodged plots supplied with 60 and 90 kg of N per ha, however, which on an

average yielded 3735 kg per ha and which may be considered as normal farmer's fields, values of — 585, + 5 and + 515 kg respectively will be found.

b. A second method which may be used when experimental fields supplied with increasing amounts of nitrogenous fertilisers are available consists of calculating the reduction in grain yield resulting from excessive nitrogen. Although this reduction may sometimes be ascribed to fertiliser interaction, it is usually due to lodging (see Fig. 3).

Under certain circumstances this method may have the same drawback as the first-mentioned, viz. when severe lodging has taken place on most plots. In that case the non-lodged plots which have to be used for calculating the yield depression will show sub-optimal yields due to nitrogen deficiency. Owing to this the calculated yield depression will be found too low. In order to overcome these difficulties the following method was introduced.

c. Parts of the crop on plots dressed excessively with nitrogen, the plants of which had generally a high tendency to lodging, were supported by ropes to keep them standing until harvest time (see Plate I). The differences in yield between the lodged and unlodged parts of the same plots were assumed to be a suitable measure of yield reduction owing to lodging. Initially the supported areas were comparatively small, viz. one meter by four, six and seven respectively (method c_1) so that the whole crop had to be taken for yield determinations. Table XIX shows the results of some typical experiments. It will be seen that the grain yields of the supported oat and wheat plants were often more than 50% higher than those of the lodged ones. This may be ascribed partly to a much increased carbon dioxide assimilation of the non-lodged plants and partly to a considerably higher grain-straw ratio. A typical feature of lodged plants is their shrivelled kernels which are the cause of the low hl weights.

Although the results of these experiments may explain the relatively high yields which may often be found when cereal crops are partly flattened, it is doubtable whether the values obtained give a true picture of yield reduction owing to lodging. It is very likely that small areas of standing plants within a lodged crop give higher yields than similar plants surrounded by non-lodged plants due to an increased illumination and CO_2-supply.

In order to eliminate this border effect in subsequent experiments

TABLE XIX

Effect of lodging on yield

Exp., crop and harvest date	Kg N per ha	Lodging index *)		Yield, q per ha		Grain as % of total yield	Hl weight, kg	Weight of 1000 grains, g
		date	date	grain	straw			
		July 17	Aug. 23					
607,	50	1	2½	34.9	56.6	38.1	76.2	42.9
summer	80(s)	0	0	40.4	64.9	38.3	77.1	45.6
wheat,	80	1½	4½	37.4	66.7	35.9	75.0	41.1
Aug. 31,	110(s)	0	0	52.3	91.6	36.3	78.0	47.6
1940	110	6	8	36.9	69.8	34.6	73.9	40.1
	140(s)	0	0	50.2	90.2	35.8	72.4	45.1
	140	6	7½	31.9	69.8	31.7	71.8	37.3
		July 6	July 31 **)					
590, oats,	50	1	10	38.7	62.1	38.4	48.2	32.0
Aug. 26,	80(s)	0	0	51.2	70.9	41.9	52.0	36.2
1940	80	1½	10	40.5	64.1	38.7	46.7	30.0
	110(s)	0	0	61.2	90.3	40.4	50.8	33.6
	110	7	10	39.6	71.4	35.7	45.6	29.3
	140(s)	0	0	65.9	90.0	42.3	51.1	33.7
	140	8	10	42.5	73.9	36.5	43.8	29.8
	170(s)	0	0	60.3	88.3	40.6	50.5	33.9
	170	6½	10	42.2	77.2	35.3	44.4	28.4

*) 0 = standing, 10 = completely lodged, s = supported.

**) July 31 the whole field was completely flattened except the supported plots which were standing.

TABLE XX

Effect of lodging on yield. Winter rye. Exp. 596, 1942

Kg N per ha	Lodging index, date **)			Yield, q per ha		Grain as % of total yield
				grain	straw	
	June 19	July 10	Aug. 10			
30(s) *)	0	0	0	32.9	69.3	32.2
30	0	0	1½	31.5 ± 1.3	61.6 ± 1.2	33.8
60(s)	0	0	2	42.2	88.6	32.3
60	2	3	6½	33.3 ± 0.3	70.5 ± 2.1	32.1
90(s)	0	0	0	41.2	82.5	33.3
90	4½	5½	7	28.6 ± 1.2	69.6 ± 2.0	29.1
120(s)	0	0	0	36.4	77.5	32.0
120	7½	7½	9	31.3 ± 0.6	73.9 ± 1.2	29.8
150(s)	0	0	0	35.8	80.3	30.8
150	8½	8	9½	23.3 ± 2.5	68.3 ± 4.6	25.5

*) s = supported plots (single values).

**) Date of harvest August 19.

TABLE XXI

Effect of lodging on yield

Experiment 612, 1941 (winter rye)					Experiment 658, 1942 (summer wheat)				
Lodging index, June 21	Kg N per ha	Grain yield, q per ha	Grain yield of unlodged plots, *) q per ha	Reduction in grain yield, q per ha	Lodging index, July 14	Kg N per ha	Grain yield, q per ha	Grain yield of unlodged plots, *) q per ha	Reduction in grain yield, q per ha
4	110	31.3	36.5(7) **)	+ 5.2	4	80	30.2	28.2(17)**)	—2.0
	110	34.2	36.5(7)	+ 2.3		80	29.7	28.2(17)	—1.5
	140	43.2	38.7(5)	— 4.5		120	26.0	27.7(14)	+1.7
	140	36.9	38.7(5)	+ 1.8					
	180	38.3	36.7(6)	— 1.6	5	160	29.2	26.7(11)	—2.5
	180	40.1	36.7(6)	— 3.4		160	26.5	26.7(11)	+0.2
	180	41.7	36.7(6)	— 5.0		160	28.5	26.7(11)	—1.8
5	85	37.9	35.8(10)	— 2.1	6	40	31.0	24.4(15)	—6.6
	140	34.0	38.7(5)	+ 4.7					
	180	33.7	36.7(6)	+ 3.0	7	160	26.7	26.7(11)	0
						160	27.8	26.7(11)	—1.1
6	85	32.2	35.8(10)	+ 3.6		160	28.4	26.7(11)	—1.7
	140	38.6	38.7(5)	+ 0.1					
	140	35.8	38.7(5)	+ 2.9	8	120	21.3	27.7(14)	+6.4
						160	25.3	26.7(11)	+1.4
6½	140	33.9	38.7(5)	+ 4.8					
					9	80	24.8	28.2(17)	+3.4
7	110	32.5	36.5(7)	+ 4.0		120	20.7	27.7(14)	+7.0
	180	35.9	36.7(6)	+ 0.8		120	18.9	27.7(14)	+8.8
						120	26.5	27.7(14)	+1.2
7½	110	31.3	36.5(7)	+ 5.2		160	22.7	26.7(11)	+4.0
	140	28.5	38.7(5)	+10.2		160	23.6	26.7(11)	+3.1
8	110	34.7	36.5(7)	+ 1.8	10	120	19.7	27.7(14)	+8.0
	180	37.4	36.7(6)	— 0.7					

) Also includes the yields of plots with lodging index 3 or lower.
) Number of plots from which the average values were calculated.

the supported plots were taken much larger so that the border plants could be discarded (method c_2).

The results of an experiment of this type are given in Table XX.

d. A fourth method of calculating the yield depressions owing to lodging, has been used in those cases where a large variation in lodging occurred resulting from different rates of sowing, different spacings, etc. Yield depressions of plots having a lodging index of 4 and higher were calculated by subtracting their yield values from average yield values of unlodged plots which had been dressed with

TABLE XXII

Effect of lodging on loss of grain yield

Exp. and year	Mean lodging index: days before harvest	Mean lodging index: erect	Mean lodging index: lodged	Reduction: q per ha	Reduction: %	Method of estimation	Exp. and year	Mean lodging index: days before harvest	Mean lodging index: erect	Mean lodging index: lodged	Reduction: q per ha	Reduction: %	Method of estimation
Winter rye							*Summer wheat*						
589, '41	51	1½	4½	7.8 ± 7.1	16.3	B	813, '44	37	½	4	4.9 ± 1.4	8.7	B
'41	51	0	4½	8.4	17.3	C_1	'44	37	0	4	4.2 ± 4.5	7.6	C_2
'43	58	2	5½	8.4	19.4	A	Gf *) 1, '43	—	0	10	16.3 ± 4.4	37.9	A
'43	58	1½	4½	9.7 ± 3.6	20.5	B	Gf 2, '53	—	0	10	14.3 ± 5.3	30.1	A
'47	20	6½	8½	4.7 ± 0.5	13.3	B	Gf 3, '53	—	0	10	10.0 ± 3.2	21.3	A
596, '42	61	0	7	10.0 ± 5.5	26.5	C_2	Gf 4, '53	—	0	10	24.0 ± 6.0	43.6	A
612, '41	45	1	8	4.2 ± 2.1	11.3	D	*Oats*						
614, '41	54	2½	4½	2.6 ± 2.1	6.1	C_2	590, '40	51	1	6	— 1.3 ± 2.0	— 3.1	B
'41	54	2½	7	8.1 ± 4.9	18.9	C_2	'40	51	0	6	18.9 ± 2.1	31.3	C_1
649, '49	63	0	8	3.8 ± 4.3	8.6	A	595, '41	15	2	6	— 5.0 ± 2.2	—13.5	B
'49	63	2½	8½	6.7 ± 0.9	15.8	B	'41	15	0	6	6.7 ± 1.7	13.8	C_1
Summer rye							598, '40	22	3	4	— 3.8 ± 1.8	— 8.8	B
612, '41	57	1	9	0.3 ± 0.4	1.0	D	'40	22	0	5	— 1.4 ± 4.7	— 3.0	C_1
Winter wheat							600, '40	22	2	9	— 5.6 ± 1.0	—11.7	A
650, '44	32	2	7	9.4	25.4	A	'40	22	0	5	4.5 ± 1.3	8.0	C_1
'44	32	½	4	9.2 ± 1.9	20.7	B	611, '41	21	4	8½	— 5.6 ± 1.1	—14.7	B
665, '43	50	0	10	9.8	25.6	A	1413, **) '53	50	0	10	13.1 ± 2.0	29.2	B
Summer wheat							Gf 5, '53	—	0	10	6.8 ± 4.1	14.7	A
588, '41	3	0	5	3.5 ± 1.9	8.1	C_2	Gf 6, '53	—	0	10	27.0 ± 7.0	60.3	A
591, '40	29	0	3	1.7 ± 0.7	3.7	C_1	*Winter barley*						
596, '40	42	0	4½	4.3 ± 1.2	16.7	C_1	759, '43	40	2	7	— 0.3 ± 2.0	— 0.6	B
607, '40	45	1½	6	3.0 ± 1.5	8.0	B	'43	40	0	7	2.2 ± 2.3	4.4	C_2
'40	45	0	6	16.9 ± 1.9	32.9	C_1	*Summer barley*						
658, '42	51	2½	5	3.7 ± 1.6	13.0	B	599, '40	42	2	8	3.4 ± 1.1	7.6	B
'42	51	½	9	5.6 ± 1.3	20.3	D	'40	42	0	8	11.8 ± 1.3	22.3	C_1

*) Gf = general field.

**) Exp. field of J. Prummel of this station.

equal amounts of nitrogen (see Table XXI). From these data it will be seen that the yields of slightly lodged crops were often higher than those of standing crops. When, however, shortly after flowering lodging indices of 7 or higher were found, depressions in grain yield varying from 10 to 30% were common.

In order to determine the average losses in grain yield for various crops the results of all experimental fields on the subject available have been brought together in Table XXII. It will be seen that a large

variation exists in the calculated values. This is partly due to the different methods of estimation used and partly to the difference in weather conditions prevailing after the crop had fallen.

The cause of yield reduction of lodged plants

Reduced carbon dioxide assimilation resulting from inadequate illumination of the green tissues is apparently the main cause of the reduced weight of lodged plants. The fact that grain formation is affected much more seriously than straw production is in accordance with this conception. The grains are formed during a relatively short period of time in which lodging frequently occurs. Straw production, however, takes place over the entire growing period.

Whether the reduced length of the highest culm internodes which is a common feature of early lodged plants may adversely affect grain formation is unknown. According to Boonstra[5]) the assimilation of the first internode contributes approximately 10 per cent towards grain formation.

In addition to the reduced carbon-dioxide assimilation, secondary factors may play a part in reducing the grain yield of lodged plants. When the plants fall before flowering, pollination may be affected as a result of which the ears remain partly deaf.

Lodged wheat plants may sometimes be heavily attacked by the semi-parasitic fungus *Septoria nodorum* which, beginning from the top, brings about necrosis and grey-brown discoloration of the chaffs. As carbon dioxide assimilation of the latter plays an important part in the grain formation (see Boonstra[5]), it will easily be seen that an early dying of these tissues appreciably effects the grain yield.

10. DISCUSSION

Lodging of cereal crops results from the combination of adverse weather conditions and an inadequate standing ability of the plants. The latter may be due to relatively weak lower internodes of the culm or to an inadequate anchorage of the plants in the soil in proportion to the weight of the upper parts of the plants. The heavier the weight of the leaves, the culm and the ear and the greater the distance of their centre of gravity to the base of the plants, the stronger should be the resistance to bending of the lower internodes

and the stronger the anchorage of the plants in the soil. This means that tendency to lodging is not a question of one particular plant property, but results from the lack of proportionality between sturdiness of the basal parts of the plants and the weight of the upper parts.

Although uprooting of plants without any bending of the lower internodes of the culm was found in a few cases to be the cause of lodging of crops dressed excessively with nitrogen, in by far the majority of the cases studied by the author the lodged plants had bent and sometimes broken lower internodes. The fact that plants dressed with excessive amounts of nitrogen were found to have a less strongly developed root system than plants with a more moderate nitrogen supply suggests that a combination of bending of the lower internodes and bending or breaking of the roots may occur rather frequently in lodged crops. It is difficult to decide, however, whether inadequate resistance of the culm base or of the roots will be the primary cause of the lodging.

From the results of the present investigation it has become clear that growing conditions during the period of elongation of the lower internodes of the cereal plants are of predominating importance in determining the tendency to lodging of the full-grown crop. These growing conditions include soil fertility, particularly available nitrogen, water supply to the plants and air humidity, and light conditions. The combination of favourable moisture conditions, relatively high temperature, cloudiness, and excessive supply of nitrogen during this part of the growing period gives rise to a very rapid growth of the young cereal plant which results in the formation of long and weak lower internodes. This is still further promoted by a dense stand of the crop. Although length of lower internodes as such has little value as an index for standing ability of the plants, it may be considered more or less as an indicator of type of growth during the early stages of the growing period. The long lower internodes often resulting from favourable growing conditions are sometimes correlated with a small culm diameter and a poor culm wall thickness. More frequently the area of lignified tissue of the sclerenchyma zone, the thickness of the lignified tissues and particularly the wall thickness of the sclerenchyma cells are reduced, whereas the development of the upper parts of the plants is more luxuriant. This gives rise to a high tendency to lodging in such a

crop. A mere wettening of the foliage and of the ears by a light rain may give rise to the flattening of the crop.

As to the influence of the various growing conditions on plant characters related to standing capacity, it has been shown that the effect of nitrogen on length and sturdiness of lower internodes is an indirect one, resulting from etiolation of the basal parts of the stem owing to the much increased leaf canopy. Apparently the same is true of water supply, since no particular effect on length of lower internodes was observed in pot experiments with widely differing moisture contents of the soil. High temperature has presumably both a direct and an indirect effect on length of lower internodes. This is concluded from the fact that in 1949 when the temperature in the spring was relatively high, exceptionally long lower internodes were formed both in the absence and presence of high nitrogen dressings. In the latter case, however, the lengths were greater than in the absence of applied nitrogen.

In addition to the indirect influence of available nitrogen on lodging resistance of cereal plants, a direct effect was found to exist viz. an adverse effect of nitrogen nutrition on the thickness of lignified tissues and particularly on the wall thickness of the sclerenchyma cells of the lower internodes of the culm. Furthermore nitrogen dressings substantially promote the development of the higher parts of the plants whilst at excessive levels a notable reduction in root development may often be observed. The latter is in agreement with the results obtained by Turner [36]) who grew barley and maize in nutrient solutions at different nitrate concentrations and with those of Goedewaagen who carried out pot experiments with wheat [13]) and field experiments on permanent grassland [16]).

The nitrogen-carbohydrate antagonism, as observed in the reduced lignification of cereal culms with increased nitrogen supply, is of general importance in plant physiology. The reduced root formation at high nitrogen levels presumably depends on the same principle. In sugar beet and potato its existence was shown by the author in field experiments with varying nitrogen dressings. In some varieties of potato the formation of tubers was largely suppressed by excessive amounts of nitrogen. At the expense of these storage tissues large amounts of protein-rich leaves were formed.

Potassium-deficient cereal plants, in addition to having a slack

appearance, possess brittle culms so that breakages occur more frequently than in the case of plants supplied with adequate amounts of potassium. As a result of this, potassium dressings will often give the impression of strengthening the plants. Although in general this was found to be true, in a number of cases plants dressed adequately with potassium lodged more severely than those with symptoms of K-deficiency. Presumably this was due to the poor development of the deficient plants in comparison with the heavy and dense crop as occurred with the full dressing. No indications were obtained that excessive amounts of potassium may exert any strengthening effect on the standing ability of cereal plants.

Length and diameter of culm internodes and in some cases culm wall thickness were found to be clearly reduced in potassium-deficient cereal plants. This will result in a weakening of the culms in the case of potassium deficiency, a conclusion which is in agreement with the results obtained by T u b b s [35]) with barley. Thickness of lignified cell walls of the sclerenchymatous ring as determined microscopically was slightly reduced in potassium-deficient culms. Chemically however, higher values for lignin were found in the K-deficient culms. It is not known whether in the latter plants "lignin" includes some other compound which is not present in the plants dressed adequately with potassium or that the increased lignin content is simply due to a decrease of other compounds in the K-deficient plants.

Phosphorus-deficient oat and wheat plants were found to have a thinner culm wall, an observation which is in agreement with the results of K i s s e l [21]). Thickness of the sclerenchymatous tissue was reduced in phosphorus-deficient wheat but not in oats. In spite of the decreased strength of phosphorus-deficient plants, liability to lodging was found to be increased by phosphate dressings on some experimental fields apparently as a result of the heavier and denser crop in the case of full dressing in comparison with the phosphorus-deficient crop.

Lodging frequently brings about a serious depression in the yield of cereal crops. In addition to a reduced quantity of grain, quality is often badly affected. The size of the yield depression depends to a large extent on the weather conditions prevailing after the crop had fallen. This presumably is the main reason for the large variation in grain losses found in the present investigation (Table XXII). Under

very wet conditions as was the case in 1953, losses of 30 per cent may frequently be found. Losses of 10–20 per cent are more common, however, whilst under favourable weather conditions values below 10 per cent will be found.

SUMMARY

The effect of nitrogen, phosphorus and potassium nutrition on lodging and yield of cereals was studied on experimental plots laid out on different soils during the years 1940 to 1949.

It was shown that favourable growing conditions prevailing during the first part of the growing period of the plants, particularly during the period of elongation of the lower culm internodes, give rise to a crop with a high tendency to lodging. These growing conditions include supply of nutrient elements, particularly of nitrogen, water supply and temperature. Ample nitrogen in combination with an optimal supply of other nutrients, an optimal water supply and a relatively high temperature at this stage will almost invariably produce a crop with a high liability to lodging. A poor illumination of the stems such as may result from shading or from a high density of the crop due to a high rate of seeding or a high proportion of weed will also decrease the standing ability of the plants. If during the period of elongation of the lower culm internodes, however, the plants suffer from a shortage of water, culms with a high standing ability will be formed.

Cereal crops with a high tendency to lodging may remain erect in the absence of adverse weather conditions during the period between ear emergence and ripening. Frequently, however, even a light rain will be sufficient to bring down such a crop. Heavy rain storms may flatten a crop which under normal climatic conditions would have maintained its upright position.

In by far the majority of cases studied by the author lodged cereal plants had bent and sometimes broken basal internodes. A combination of bending of the lower internodes and bending or breaking of the roots presumably may frequently occur in lodged crops.

An comprehensive study was made of the effect of nitrogen dressings on a number of plant properties related to the standing ability of cereal plants. Plants supplied amply with nitrogen, which in general have a high tendency to lodging, were found to have longer lower culm internodes than those grown on the same field with a low or moderate nitrogen supply. The upper two internodes of the former plants were often considerably shorter, particularly when lodging had taken place before the plants had reached their full height. The number of measurable internodes tends to increase with increased nitrogen supply.

With an increased rate of nitrogen supply, the diameter of the upper culm internodes was often found to be considerably increased; the lower internodes, however, had equal or smaller diameters.

In a number of cases the culm wall thickness of lodged plants was found to be considerably smaller than that of non-lodged plants. In some other cases, however, no difference or even the reverse was found.

The thickness of the sclerenchymatous ring in a number of cases tended to decrease with increased nitrogen supply. Thickness of sclerenchyma cell walls and area of lignified tissue in the sclerenchyma zone were found to be appreciably reduced by ample nitrogen. The number of vascular bundles was unaffected by nitrogen nutrition but lignification of these bundles and of the outer layers of parenchyma was reduced by large dressings with nitrogenous fertilisers.

Weight per cm of basal culm length was frequently found to be lower in plants treated with ample nitrogen.

The development of the root system was likewise found to be clearly affected by nitrogen dressings. Lodged plants supplied with excessive amounts of nitrogen had a less sturdy root system with less heavily lignified roots.

The results of the latter experiments have shown that weakness of the basal parts of a cereal plant may be brought about by the poor development of various plant characters. Since tendency to lodging depends on a disproportionality between the weight of the aerial parts of the plant and the resistance to bending and breaking of the basal culm internodes and the roots, it can be concluded that a high liability to lodging may, in different cases, be due to different causes.

In pot experiments with different degrees of illumination and in field experiments with different rates of seeding and spacing it was found that the unfavourable effect of excessive amounts of nitrogen on the strength of the basal parts of cereal culms has to be attributed partly to an indirect shading effect and partly to a direct nutritional effect. Elongation of the lower internodes depends entirely on the shading effect whilst reduction of culm diameter, of culm wall thickness and of lignification may be brought about by shading as well as by a direct nitrogen effect.

Although the straw of potassium-deficient cereal plants is more brittle than that of plants supplied with adequate amounts of potassium, more severe lodging in the latter was sometimes observed. This was presumably due to the heavier and denser crop in the case of fully dressed plants. No effect of excessive amounts of potassium on strength of culms was observed.

K-deficient plants in general had shorter and thinner internodes than plants supplied normally with potassium. The thickness of the sclerenchyma cell walls tended to be slightly reduced in the case of potassium deficiency.

Phosphorus-deficient plants lodged less severely than those dressed amply with phosphate, apparently due to a poorer development. The number of vascular bundles was found to be reduced in phosphorus-deficient oat and wheat plants.

Liming an acid peaty soil was found to increase the tendency to lodging of a cereal crop growing on this soil, due to the improved nitrogen supply of the plants.

A poor soil structure was found to give no increased liability to lodging of cereal plants.

For estimating the reduction in grain yield due to lodging different methods have been employed, viz. *a*) comparison of the yields of lodged and non-lodged areas in the same field, *b*) calculation of the reduction in grain yield at high nitrogen dressings on fertiliser experimental fields, *c*) comparison of the yields of lodged and non-lodged (supported) parts of plots dressed with high amounts of fertiliser nitrogen, *d*) comparison of the yields of cereal plots with a different lodging index due to a different rate of sowing and a different spacing of the plants.

The losses in yield of grain due to lodging varied from 0 to 60 per cent. In some cases even negative values have been found. This large variation was due partly to the different methods of estimation and partly to the difference in weather conditions prevailing after the crop had fallen.

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